GREENHOUSE GAS EXCHANGE AND NITROGEN CYCLING IN SASKATCHEWAN BOREAL FOREST SOILS

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ABSTRACT

Despite the spatial significance of Canada's boreal forest, there is very little known about greenhouse gas emissions within it. The primary objective of this project was to study the atmosphere-soil exchange of CH_4 and N_2O in the boreal forest of central Saskatchewan. In the summers of 2006 and 2007, greenhouse gas emissions were measured along transects in three different mature forest stands (trembling aspen, black spruce and jack pine) using a sealed chamber method. In addition, the gross rates of mineralization and nitrification, and the relative contribution of nitrification and denitrification to N_2O emissions, were measured at the trembling aspen site using a stable isotope technique in which ^{15}N-enriched nitrate and ammonium were injected into intact soil cores. The amount of ^{14}N found in the labeled pools was used to measure the gross rates, and the amount of ^{15}N found in the emitted N_2O was used to determine the relative contribution of the different N pathways to total N_2O emissions. Results indicated that the jack pine and black spruce sites were slight sinks of CH_4 (-1.23 kg CH_4-C ha^{-1} $yr^{-1}$and -0.17 kg CH_4-C ha^{-1} yr^{-1} respectively in 2006 and -0.95 kg CH_4-C ha^{-1} $yr^{-1}$and 0.45 kg CH_4-C ha^{-1} yr^{-1} respectively in 2007), whereas the trembling aspen site was a net source (46.7 kg CH_4-C ha^{-1} yr^{-1} in 2006 and 196.0 kg CH_4-C ha^{-1} yr^{-1} in 2007). All three sites had very low cumulative N_2O emissions, ranging from -0.02 to 0.14 kg N_2O-N ha^{-1} yr^{-1} in both years. Of the environmental controls examined for CH_4, consumption at the jack pine site was correlated positively with organic carbon and negatively with water-filled pore space. Black spruce CH_4 emissions were correlated negatively with both organic carbon and clay content, and emissions at the trembling aspen site were positively correlated with soil temperature and organic carbon, while also related to the presence of standing water (2006 and 2007 had very high precipitation, causing a high water table and ponding in depressions). The N_2O emissions were not correlated with any of the environmental parameters measured at the jack pine or black spruce sites, but clay content was positively related to emissions at the trembling aspen site. The ^{15}N results indicated that N cycling at the trembling aspen site was very rapid, allowing little N to escape the system as N_2O; the majority of emissions that did occur were due to a nitrification-related process.

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1. INTRODUCTION

The atmospheric greenhouse gases methane (CH_4) and nitrous oxide (N_2O) are the third and fourth greatest contributors to the greenhouse effect (after water vapor and carbon dioxide). Although their concentrations are much lower than CO_2, the global warming potentials of CH_4 and N_2O are approximately 25 and 300 times greater, respectively (Dalton and Brand-Hardy, 2003; Driscoll, 2003). The concentration of the two gases is currently increasing in the atmosphere; since pre-industrial times CH_4 has increased by 148% and N_2O has increased by 18% (IPCC, 2007).

Emissions of CH_4 and N_2O contribute to global warming by radiative forcing (absorption of infrared radiation, some of which is emitted back towards earth) and atmospheric photochemistry (reactions producing compounds which exacerbate thinning of the stratospheric ozone layer) (Whalen, 2005). Once released into the atmosphere, greenhouse gases absorb radiation of a given wavelength (dependent on the gas) and cause warming to occur. What makes CH_4 and N_2O effective greenhouse gases, is their ability to absorb radiation at different wavelengths than other gases in the atmosphere. Methane is removed from the atmosphere by reacting with hydroxyl (OH^-) radicals in the troposphere. However, in doing so it can react to form both CO_2 and water vapor, which further its contribution to the greenhouse effect (Whalen, 2005). Nitrous oxide is not removed in the troposphere, but must instead travel to the stratosphere where it can be destroyed by solar ultraviolet radiation. This means that the gas will remain in the atmosphere longer than most other gases, increasing its total warming effect. When it is eventually destroyed, the reaction can form ozone-depleting radicals such as nitric oxide (NO) and chlorine (Cl) (IPCC, 2001).

Climate change is characterized by temperature rise, sea level rise and extremes in the hydrologic cycle. It may cause more frequent and intense climate events, such as storms, droughts and floods (IPCC, 2007; Lemmen and Warren, 2004). In Canada, such changes are evident in the north, where impacts include decreases in sea ice and glacier extent, increases in the active layer of permafrost, and intensified coastal erosion

(Environment Canada, 2003). These changes affect local residents by making travel more difficult and dangerous, and affecting access to traditional hunting grounds. A gradual increase in temperature could benefit other parts of Canada, such as boreal ecosystems, by increasing growing season length and decreasing the number of deaths from extreme cold. However, many boreal areas are already experiencing a disproportionate number of negative effects, such as changes in water flow, fish populations, tree distribution, forest fires, drought, and agricultural and forest pests (Lemmen and Warren, 2004).

Although emissions can come from several sources, such as combustion from various industrial processes, the majority of N_2O emissions (70%), and a significant amount of CH_4 emissions (15-37%) come from the soil (IPCC, 2001). Specifically, agriculturally-related additions of nitrogen to the terrestrial environment have caused the most significant increases in N_2O emissions, while most CH_4 comes from a combination of natural and man-made wetlands. However, accurate estimates are hindered by the lack of information about those ecosystems across the globe that are not under direct management, but may be indirectly affected by anthropogenic practices (Whalen, 2005). In particular, the boreal forest ecosystem of Canada, although spatially significant and a major resource for several industries (power, forestry, tourism) is not well understood from a greenhouse gas perspective. Therefore, in order to better understand and manage CH_4 and N_2O emissions, it is first necessary to quantify them, and determine what controls their emissions from soils in different landscapes.

The two objectives of this study are: (1) to create an inventory of CH_4 and N_2O emissions from three mature boreal forest stands, while concurrently studying some possible environmental and landscape controls on those emissions, and (2) to examine nitrogen cycling in detail at a boreal trembling aspen stand, to determine the rates of nitrogen cycling within the soil and which pathways lead to N_2O emissions.

2. LITERATURE REVIEW

2.1 Methane processes

Methane can be emitted through both anthropogenic and natural processes. Anthropogenic sources include artificially flooded soils used for cultivation, fossil fuels (natural gas and coal mining), biomass burning and landfills. Natural sources consist of wetlands, tundra, ruminants, termites and oceans. Of all of these sources, though, 70% of emissions come from the soil (Ritchie et al., 1997). In the soil environment, depending on microsite conditions and which microbial communities are present, CH_4 can be both produced and consumed. In fact, between 43% and 90% of the CH_4 produced in the soil is consumed before it can be emitted to the atmosphere (Liebner and Wagner, 2007). The atmospheric concentration at any given time or place is the balance between the sources and sinks of CH_4 (Whalen and Reeburg, 2000).

Methane is produced from organic matter by methanogenic bacteria in anaerobic conditions, such as submerged soils. This conversion has several steps, most of which require different populations of micro-organisms (Figure 1). The first group is hydrolytic microflora, which break down complex polymers into simpler monomers. Next, fermentative microflora use the monomers to produce volatile fatty acids, organic acids, alcohols, H_2 and CO_2. These metabolites may then undergo acetogenesis via syntrophic or homoacetogenic microflora. Finally, methanogens convert the simple compounds (H_2 and CO_2 or acetate) into CH_4. Although there are only a few methanogens that can use acetate as a carbon and energy source, acetotrophy (acetate fermentation) usually accounts for about two-thirds of CH_4 production, with CO_2 reduction with H_2 making up the balance (Whiticar et al., 1986). Methanogenesis, the term used to describe both of the CH_4-producing pathways, is strictly anaerobic and requires low oxido-reduction potentials (Le Mer and Roger, 2001; Whalen, 2005). Methanogens exposed to O_2 have been reported to cease CH_4 production for up to 48 hours after anoxic conditions return (Whalen and Reeburg, 2000).

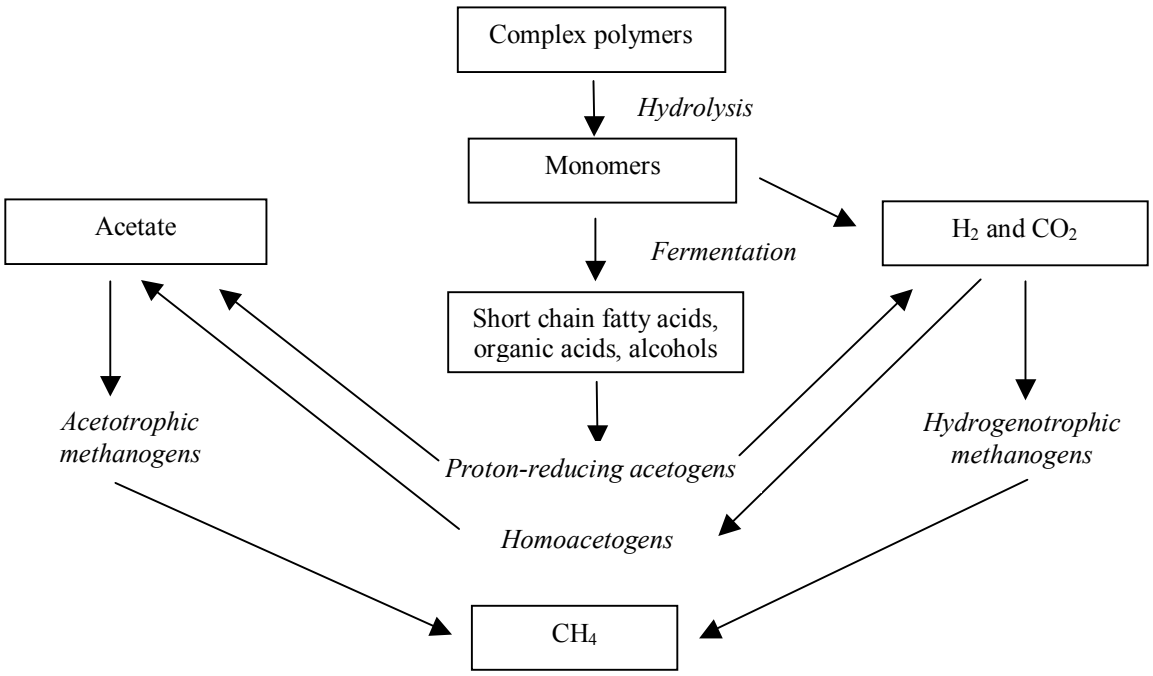


Figure 1. The formation of methane from organic matter (adapted from Whalen, 2005).

Methanogens are relatively ubiquitous in soils, including upland and wetland forest soils (Mayer and Conrad, 1990). In peatland, the acetate fermentation pathway usually occurs in shallow subsurface regions that have a ready supply of labile substrates, whereas CO_2 reduction with H_2 is more prevalent at depth, in the older, less reactive peat (Hornibrook et al., 1997). It is site conditions, rather than the type of methanogens present, that control CH_4 flux. Basiliko et al. (2003) examined the methanogen population at two northern peatland sites with highly contrasting CH_4 flux rates, and found that although the size of the populations differed, the diversity at each site was similar and included methanogens from many of the same families. The site exhibiting higher CH_4 flux simply had a few populations that were much more dominant than the others. This corresponds well with earlier work by Mayer and Conrad (1990), who observed the same phenomena: although methanogens could be found in many different soils, they remained a small percentage of the overall microbial community until conditions were more favorable for their growth.

Oxidation or consumption of CH_4 is known to occur in the soil in three ways: high-affinity oxidation, low-affinity oxidation and anaerobic oxidation. High-affinity oxidation occurs when CH_4 concentrations are close to those found in the atmosphere (<12 ppm); this process is thought to be responsible for 10% of overall consumption but beyond that it is poorly understood (Le Mer and Roger, 2001). Low-affinity oxidation occurs when CH_4 concentrations are higher than 40 ppm, and this process is performed by methanotrophs. These organisms occur in soils with pH higher than 4.4, and can use CH_4 as both a C and energy source. They have been found to be active in oxidized soil layers, aerobic rhizospheres and inside plant roots and leaves; the limiting factor to their activity is oxygen availability. Anaerobic oxidation has been well-documented in marine soils (Hoehler et al., 1994; Valentine, 2002), but the mechanism for its occurrence in freshwater wetlands has not yet been ascertained. However, there is strong evidence that it is a present - and in some cases significant - process in these regions (Smemo and Yavitt, 2007). In marine soils, the pathway is believed to involve electron transfer between CH_4-oxidizing archaea and sulfate-reducing bacteria (Valentine, 2002).

Studies have shown that populations of methanotrophs will increase in forest soils as methane concentration in the immediate atmosphere increases (Bender and Conrad, 1992). Although this ideally serves to reduce atmospheric CH_4, it may not necessarily be beneficial in terms of net greenhouse gas fluxes in stands with significant amounts of inorganic N in the soil. Bodelier and Frenzel (1999) demonstrated that, due to the homogeneity of the CH_4 oxidation enzyme (methane monooxygenase) and the NH_4^+ oxidation enzyme (ammonia monooxygenase), methanotrophs could significantly contribute to nitrification. Nitrification can in turn lead to the emission of N_2O (Section 2.2), which is the more potent of the two gases. In fact, CH_4 oxidation has been linked to nitrification rates in some regions. Steudler et al. (1996) found that Brazilian forest soils with high nitrification rates would have low CH_4 oxidation because nitrifiers were dominant, whereas soils with low nitrification rates would exhibit high CH_4 oxidation because methanotrophs were dominant.

Many environmental controls affect CH_4 emission. Soil properties that change the oxygen status of the soil, such as density and water content, can alter the amount of methanotrophic activity in an area. The chemistry of the soil or water can play an important role if there is a significant amount of nitrate, ferric iron or sulphate. The microbes that reduce these compounds compete with methanogens for acetate and electrons (Smemo and Yavitt, 2007). Climatic conditions may also play an important role. Methane emissions from swamps and peatlands in Canada have been shown to increase by almost seven times when temperature increases from 10 to 23°C (Moore and Dalva, 1993). In some cases, the vegetation of a given area can significantly affect whether or not CH_4 is emitted. Plants with an aerenchyma, tissue that allows gases to circulate within the plant, facilitate CH_4 emission to the atmosphere. Plants without an aerenchyma tend to have more oxidation activity in the rhizosphere, which decreases the amount of CH_4 reaching the surface (Le Mer and Roger, 2001).

2.2 Nitrous oxide processes

The nitrogen cycle is a complex series of reactions involving a host of processes occurring both above and below the ground. There are several soil processes that can produce N_2O: denitrification, nitrifier denitrification, nitrification and

chemodenitrification; the basic pathways for these are shown in Figure 2. Depending on the process that is occurring, there are a number of environmental controls that may be particularly conducive to N_2O emissions.

Denitrification is the series of reactions that reduces nitrate (NO_3^-) to nitrogen gas (N_2). These reactions are predominantly carried out by microbes that are facultative anaerobes, which use NO_3^- as an electron acceptor instead of oxygen (Wrage et al., 2001). This often occurs when the soil reaches levels beyond 60% water-filled pore space (Lemke et al., 1998), as the diffusion of oxygen is slowed by the water in the soil pores, creating anaerobic conditions (Renault and Stengel, 1994). Nitrous oxide is only an intermediate in the overall denitrification series, but under certain conditions the process stops at N_2O rather than proceeding to N_2. Soils with low pH and some oxygen availability (rather than being entirely anaerobic) are more likely to have increased N_2O emissions, because the enzyme that catalyzes the final reaction from N_2O to N_2 is inhibited by these conditions (Wrage et al., 2001). When alkaline soils approach saturation and there is no longer any oxygen inhibiting the nitrous oxide reductase enzyme, N_2 is more likely to be produced (Veldkamp et al., 1998). If there are large amounts of NO_3^- available in the soil, this may increase N_2O emissions, because NO_3^- is preferred over N_2O as an electron acceptor. Denitrifiers are generally heterotrophs, so denitrification is less likely to occur in areas with low levels of available organic carbon (Wrage et al., 2001).

Nitrifier denitrification is a series of reactions that starts out by oxidizing NH_3 to NO_2^-, and then reduces NO_2^- to either N_2O or N_2. This set of reactions is carried out by microorganisms known as autotrophic ammonia-oxidizers. The main difference between this series and denitrification is that NO_3^- is not produced, and as autotrophs, these microbes do not require organic C. Environmental controls that increase the activity of this group are similar to those of the denitrifiers, with regards to low pH and low oxygen availability. However, since this group is autotrophic, they are more likely to be a significant source of N_2O in areas with low organic C and high N availability. This group is not as well understood as the denitrifiers, so other controlling factors are not yet known (Wrage et al., 2001).

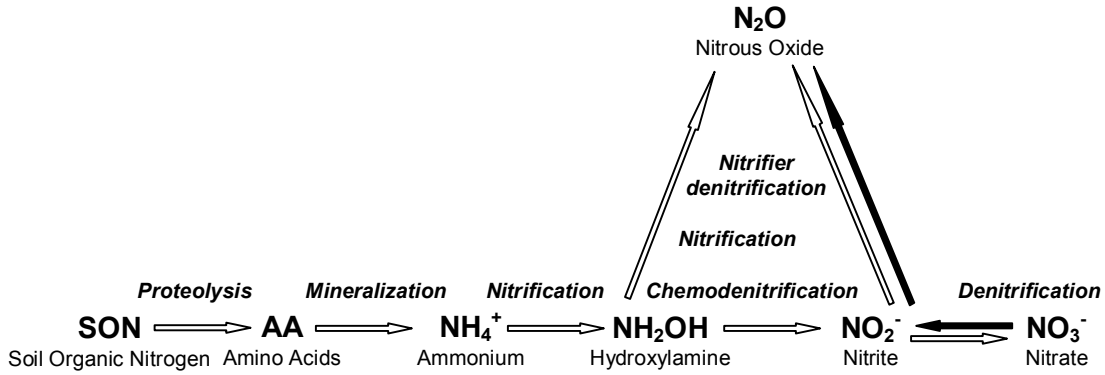


Figure 2. A simplified diagram of the nitrogen cycle, showing the major pathways that result in the emission of nitrous oxide; adapted from Ambus et al. (2006).

Nitrification, the oxidation of ammonium (NH_4^+) or ammonia (NH_3) to NO_3^-, can result in N_2O emissions through chemodenitrification or the incomplete oxidation of NH_2OH by microorganisms (Wrage et al., 2001). Chemodenitrification is the chemical decomposition of oxidation intermediates like hydroxylamine (NH_2OH) or nitrite (NO_2^-) with other compounds (may be organic or inorganic). It is a non-biological process that sometimes results in N_2O, although more commonly in NO. This process is closely linked with nitrification, since that is where the intermediates originate. Nitrification is carried out by both autotrophic and heterotrophic microorganisms. Autotrophic nitrifiers get energy from the oxidation of ammonium and assimilate C from CO_2, while heterotrophic nitrifiers (this can include both bacteria and fungi) rely on organic substances for food, but may get a competitive advantage from the process of nitrification (Paavolainen, 1999). The main environmental control known to intensify the nitrification-related emissions of N_2O is acidic conditions (Wrage et al., 2001). However, Poth and Focht (1985) also suggest that it may be a strategy used by nitrifiers to decrease oxygen competition from denitrifiers by denying them substrate, as well as a method to reduce production of nitrite when it is accumulating to toxic levels. As mentioned in Section 2.1, methanogens may also inadvertently contribute to the nitrification process.

Temperature is known to be an important control of microbial processes. Although many microbes are inhibited by low temperatures, it has been shown that N_2O emissions are not always directly related to changes in temperature. In some cases, N_2O will increase as temperature decreases, and this is thought to possibly relate to the inhibition of the nitrous oxide reductase enzyme (Wagner-Riddle and Thurtell, 1998). However, although it is not always directly related to emissions, temperature is considered to be an important control in conjunction with other environmental parameters (Yates et al., 2006).

2.3 Nitrogen cycling

Since N_2O can be generated as a result of both the nitrification and mineralization processes, it can be better understood if those rates are quantified and the pathway responsible for the majority of emissions known. This can be done using ^{15}N, a

stable nitrogen isotope, to capture how quickly these pools turn over and to trace which pool is responsible for the majority of emitted N_2O.

Traditionally, mineralization and nitrification have been measured using varied-length incubations of soil in either a laboratory setting or buried in the field; such incubations provide the net change in inorganic N pools over a given time period (Raison et al., 1987). Using ^{15}N to measure gross rates differs from the measurement of net rates, in that it can measure how much N is flowing through the NO_3^- and NH_4^+ pools, rather than simply the differences in the pools between two points in time. This becomes especially significant in regions where there are inherently low pools of N, but N turnover is rapid. In cases such as these, there may be a steady amount of N flowing through the system, although the inorganic pool sizes (and therefore net rates) change very little (Davidson et al., 1992).

To measure gross rates, the inorganic N pools are labeled with ^{15}N so that movement through them can be traced. In general, this involves adding a label to the product pool and measuring how much it is diluted by unlabeled N over a given time. Although it is possible to use ^{15}N as a tracer by labeling the substrate pool, the dilution method has the advantage of not inducing an artificial increase in cycling by supplying additional substrate. This becomes crucial in forest systems that are inherently low in N, where any amount of added N becomes a significant percentage of the total N in the soil (Hart et al., 1994). The technique with which the ^{15}N is added can vary between studies. In this study, intact soil cores are injected with solutions of $^{15}NO_3^-$ or $^{15}NH_4^+$ as in Davidson et al. (1991). Others have used dried and ground soil, and added the solution directly to the surface or injected it into re-packed soil cores (Hogberg et al., 2006). This has the advantage of homogeneous samples that can be consistently replicated and uniformly labeled. However, it eliminates soil processes that occur in developed microsites, which are believed to play a significant role in nutrient cycling (Schimel and Bennett, 2004). In addition, research has shown that a completely homogenous label is not required to obtain meaningful results using ^{15}N techniques. Davidson et al. (1991) found that uneven distribution of the label in soil did not significantly alter the results unless there were areas that received very high doses while others received none at all.

2.4 Boreal forest overview

2.4.1 CH_4 and N_2O emissions

The boreal forest ecosystem covers 35% of Canada and makes up 77% of the nation's total forested land. In its entirety, it makes up 33% of the world's forest area (Environment Canada, 2003). Despite its spatial significance, however, there have been very few Canadian studies focused on greenhouse gas emissions from this ecosystem. There has been a multitude of work done in Europe, and the results from several of these studies are summarized in Table 1, together with the available Canadian data. However, the relevance of European data in Canadian forest ecosystems is questionable, since the boreal forest in Europe has a long history of harvesting and management that Canada does not share (Busenberg, 2004). Despite significant differences in land use history and nitrogen deposition levels, though, these studies provide an excellent framework within which this project can be placed.

As shown in Table 1, CH_4 emissions from boreal soils are quite varied, but when looking at controls on those emissions, several themes emerge. Methane fluxes are strongly regulated by the presence or absence of methanotrophs, which are generally found in the upper 10-20 cm of soil or peat (Whalen et al., 1992; Berestovskaya et al., 2005). The activity of both methanotrophs and methanogens are dependent on temperature, pH, water level, water flow and nutrient availability (Berestovskaya et al., 2005; Rask et al., 2002; Saarnio et al., 2007; Arnold et al., 2005). Also significant is the type of wetland measured; CH_4 production is generally higher in fens than in bogs, likely due to the higher nutrient status of fens as compared to bogs (Moore and Knowles, 1990; Regina et al., 1996).

The variation in N_2O emissions from Table 1 is remarkably small, but as all of the sites were mature, with no recent anthropogenic disturbance, it is likely they all come from relatively remote areas that would not receive as much atmospheric deposition as those closer to major centers. As with CH_4, it was noted that most of the N_2O consumption or production came from the upper part of the soil (Pihlatie et al., 2007). This was attributed to presence of the three major requirements for N_2O production: a C source, an N source and - in the case of denitrification - anoxic

Table 1. A summary of studies including cumulative nitrous oxide (N_2O) and/or methane (CH_4) emissions from unmanaged boreal forest and tundra soils around the world. All studies used *in situ* static chambers to measure emissions.

Location	Site/Vegetation	Soil	N_2O flux (kg N_2O-N ha^{-1} yr^{-1})	CH_4 flux (kg CH_4-C ha^{-1} yr^{-1})	Reference
Sask.	Black spruce	Organic	-	21.1 to 270.3	Rask et al. (2002)
Alberta	Open fen	Organic	-3.5 to 2.1	-	Wray & Bayley (2007)
Quebec	Open fen	Organic	-	13 to 99	Moore & Knowles (1990)
	Ombrotrophic bog	Organic	-	<1.5	Moore & Knowles (1990)
Alaska	Black/white spruce	Brunisol	-	-2.3 to -2.0	Whalen et al. (1992)
Finland	Bog	Organic	-	20 to 40	Alm et al. (1999)
	Minerotrophic fen	Organic	-	18.8 to 766.6	Huttunen et al. (2003)
	Scots pine	Podzol	-0.67 to 0.39	-	Pihlatie et al. (2007)
	Minerotrophic fen	Organic	-0.06 to 0.46	-	Regina et al. (1996)
	Ombrotrophic fen	Organic	-0.07 to 0.06	-	Regina et al. (1996)
Russia	Dwarf birch	Cryosol	-	4.4 to 111.3	Berestovskaya et al. (2005)
Sweden	Alder	Organic	0.32 to 0.95	33.7 to 80.1	Arnold et al. (2005)
	Raised bog	Organic	-	-2 to 161	Waddington & Roulet (2000)

conditions in the soil (Wray and Bayley, 2007). Regina et al. (1996) reported that N_2O emissions were positively correlated with the number of nitrite oxidizers, nitrification potential, N, P and Ca content, and pH of the soil. They also observed that emissions increased after a lowering of the water table, but only in minerotrophic sites.

It is notable in Table 1 that there has been very little emphasis placed on upland forest soils. Methane, in particular, has the potential to vary significantly between and within study sites, and yet there were very few measurements of CH_4 from soils in non-peatland regions. The relative lack of anthropogenic disturbance in Canadian forest ecosystems is unique for the world's boreal forests, allowing us to ascertain the undisturbed gas emission levels from this ecosystem. This advantage should be exploited in both upland and lowland regions within the boreal forest, since knowing these background values could be very important as anthropogenic practices change the structure and functioning of the boreal forest in the future.

2.4.2 Gross nitrogen cycling

In order to understand what controls gas emissions, it is important to go beyond simply measuring N_2O emissions, and include investigations of N cycling in the soil. With current concern regarding how climate change will affect greenhouse gas emissions, improving our knowledge of N-cycling in the boreal forest will contribute to our ability to predict how or if the currently low N_2O emissions coming from the boreal landscape will be altered. It will also aid in predicting how eventual increases in acid rain and N deposition might affect these areas and provide insight into amelioration possibilities. As well, knowledge of how N cycles through pristine boreal forest soils could provide a threshold for comparison with forest soils in areas managed for forestry or agriculture, to assess whether harvest disturbance significantly changes N cycling.

There have been some measurements of gross N cycling in the boreal forest of Canada, and several studies have been conducted in European boreal soils. As shown in Table 2, undisturbed boreal forest soils tend to have higher gross rates of mineralization than nitrification. This suggests that boreal plants have adapted to using NH_4^+ as a N source, possibly as an adaptation to keep N from escaping the system, as NO_3^- is more prone to leaching than NH_4^+ (Raison, 1979). Although the mineralization rates are quite

Table 2. A summary of studies reporting measurements of gross mineralization and nitrification rates (some net rates are included for comparison) from boreal forest soils in Canada and Europe.

Country	Forest type	Stand Age (yr)	Soil Type	Mineralization (mg NH_4-N kg^{-1} d^{-1})	Nitrification (mg NO_3-N kg^{-1} d^{-1})	Reference
Canada	Mixed	>70	Gray Luvisol	0.00 to 0.02 (net)	undetectable (net)	Carmosini et al. (2002)
	Mixed			1.28 to 2.06	undetectable	
	Peatland	75-120	Humisol	18 to 19	0 to 2	Westbrook et al. (2004)
	Coniferous		Dystric Brunisol	14 to 19	0 to 2	
	Peatland	75-120	Humisol	-0.11 to -0.01 (net)	0.01 (net)	Westbrook et al. (2006)
	Coniferous		Dystric Brunisol	-0.05 to 0.03 (net)	0.01 to 0.03 (net)	
Sweden	Deciduous	-	Dystric Brunisol	2.7 to 23	0.1 to 0.8	Bengtsson et al. (2003)
	Scots Pine	53	(N-limited)	15 to 17	-	Chen and Hogberg (2006)
			(N-saturated)	47 to 52	-	
	Scots Pine	130	Orthic Podzol	9.3 to 16.3	undetectable	Hogberg et al. (2006)
	Norway Spruce			34.4 to 63.2	undetectable	

varied, it is notable that nitrification is always negligible. Nitrous oxide emissions can only occur if nitrification is occurring (whether they come from the nitrification-related or denitrification pathways - Section 2.2), so the very low nitrification rates in all of the soils in Table 2 provide an excellent context for the low N_2O emissions in Table 1.

2.5 Soils and landscapes of Saskatchewan's boreal forest

Saskatchewan's land base is 53% forested and of this, 38% is managed for timber production (J. Kowalski, personal communication, 2008). There are three predominant tree species found in the mid-boreal upland ecoregion of Saskatchewan where this study takes place: jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* [Mill.] B.S.P.) (Latin names from Beckingham et al., 1996). Of Saskatchewan's total tree species composition, 20% is jack pine, 37% is trembling aspen and 19% is black spruce (J. Kowalski, personal communication, 2008); each of these tree species is used for commercial purposes. Jack pine trees are used to produce both lumber and wood chips; in Saskatchewan they account for 36% of the coniferous trees harvested. Trembling aspen is commonly utilized for oriented strand board and black spruce is used mostly for pulpwood (Saskatchewan Forest Centre, 2006).

Jack pine trees can withstand harsher climatic conditions than any other pine species and are the most widely distributed pine species of Canada's boreal forest (Saskatchewan Forest Centre, 2006). Stands of almost pure jack pine most often occur on coarse-textured glaciofluvial or eolian parent material, where, due to the parent material, the soils tend to be acidic, with poor nutrient status (Johnson et al., 1995). These harsh growing conditions force the trees to be relatively widely spaced, with very little understory. The forest floor in most jack pine stands is dominated by reindeer lichen (*Cladina spp.*). Other characteristic species include bearberry (*Arctostaphylos uva-ursi* [L.] Spreng.), blueberry (*Vaccinium myrtilloides* Michx.), bog cranberry (*Vaccinium vitis-idaea* L.), wild lily-of-the-valley (*Maianthemum canadense* Desf.) and Schreiber's moss (*Pleurozium schreberi* [Brid.] Mitt.). In transitional areas with slightly more fine-textured material, green alder (*Alnus crispa* [Ait.] Pursh) and sand heather (*Hudsonia tomentosa* Nutt.) also appear. Although jack pine trees generally colonize

after a fire and are later succeeded by spruce, the conditions in many areas inhibit the intrusion of spruce between fires, allowing the pines to create a fire climax community (Beckingham et al., 1996; Johnson et al., 1995).

Black spruce stands usually establish themselves on organic or peaty-phase soils, in level or depressional areas with slow drainage or high water tables. They can be found in both treed bogs and fens, where stagnant or very slow-moving water results in a poor to very poor nutrient status (Beckingham et al., 1996). Although black spruce can grow as high as 25 to 30 m, those found in poorly drained areas grow very slowly and reach a maximum of 10 to 20 m in height (Saskatchewan Forest Centre, 2006). In bogs, common understory shrubs and forbs include Labrador tea (*Ledum glandulosum* Nutt.; *Ledum groenladicum* Oeder), bog cranberry (*Vaccinium vitis-idaea* L.) and cloudberry (*Rubus chamaemorus* L.). There are often numerous species of mosses, the most common of which are peat moss (*Sphagnum spp.*), Schreber's moss (*Pleurozium schreberi* [Brid.] Mitt.) and stair-step moss (*Hylocomium splendens* [Hedw.] B.S.G.), as well as an abundance of reindeer lichen (*Cladina spp.*). In the slightly more nutrient-rich fens, the canopy is often a mixture of both black spruce and tamarack (*Larix laricina* [Du Roi] K. Koch.). The understory in this type of fen is not as well isolated from the water table, and is therefore less likely to include lichens; instead it includes sedges and different mosses, such as tufted moss (*Aulacomnium palustre* [Hedw.] Schwaegr.). Barring disturbance, treed poor fens will succeed to treed bogs, but succession is very slow, sometimes taking thousands of years (Beckingham et al., 1996; Johnson et al., 1995).

Trembling aspen stands are generally found on moderately fine to fine-textured till or glacio-lacustrine parent materials. One of the most common stands in the mid-boreal upland ecoregion, they tend to have adequate nutrient levels, and an intermediate amount of moisture, as compared to the extremes seen in jack pine and black spruce stands (Beckingham et al., 1996). The predominantly deciduous trembling aspen stands usually have an abundant and diverse understory. Characteristic shrubs include beaked hazelnut (*Corylus cornuta* Marsh.), green alder (*Alnus crispa* [Ait.] Pursh), prickly rose (*Rosa acicularis* Lindl.), low-bush cranberry (*Viburnum edule* [Michx.] Raf.) and twin-

flower (*Linnaea borealis* L.). There are numerous forbs, the most common being wild sarsaparilla (*Aralia nudicaulis* L.), bunchberry (*Cornus canadensis* L.) and dewberry (*Rubus pubescens* Raf.). In moist areas, marsh reed grass (*Calamagrostis canadensis* [Michx.] Beauv.) is also common. Trembling aspen are often pioneer species later succeeded by white spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* [L.] Mill.) where seeds for them exist. As this occurs, the increased canopy cover inhibits the growth of the understory and more mosses tend to flourish (Beckingham et al., 1996; Johnson et al., 1995). The trembling aspen stand in this study was selectively harvested for white spruce in the past, decreasing the spruce seed stock and resulting in the formation of an old growth trembling aspen stand (Weir and Johnson, 1998).

3. GREENHOUSE GAS FLUX AND NITROGEN CYCLING IN THE BOREAL FOREST

3.1 Introduction

Despite the spatial significance of Canada's boreal forest, there is very little known about greenhouse gas emissions within it. The three dominant tree species in Saskatchewan's boreal forest are jack pine, black spruce and trembling aspen (J. Kowalski, personal communication, 2008). Despite this, review of available literature supplied only a single study which reported CH_4 emissions from an undisturbed black spruce stand (21.1 to 270.3 kg CH_4-C ha^{-1} yr^{-1}; Rask et al., 2002), and there were no studies from undisturbed trembling aspen or jack pine stands. Several values are available in the literature for undisturbed Canadian peatlands, ranging from <1.5 up to 99 kg CH_4-C ha^{-1} yr^{-1} and -3.5 to 2.1 kg N_2O-N ha^{-1} yr^{-1}(Moore and Knowles, 1990; Wray and Bayley, 2007), but these only have limited relevance for the boreal forest as a whole. European research is more extensive but follows the same trend, with a strong focus on boreal wetlands. Emissions reported from undisturbed regions in Europe range from -2 to 767 kg CH_4-C ha^{-1} yr^{-1} and -0.06 to 0.95 kg N_2O-N ha^{-1} yr^{-1} (Arnold et al., 2005; Huttunen et al., 2003; Regina et al., 1996; Waddington and Roulet, 2000).

As interest into possible effects of climate change increases, simply knowing the magnitude of greenhouse gas emissions from a site will be inadequate; one must also understand the underlying processes involved. Rates of N cycling through the soil have been successfully correlated to N_2O emissions (Stevens et al., 1997), and could reveal much about overall N dynamics of the forest. However, such rates have yet to be quantified within most regions of the boreal forest in Canada. Current values from mixedwood and peatland soils (Luvisols, Brunisols and Organic soils) report extremely varied mineralization rates, from 1.28 up to 19 mg NH_4-N kg^{-1} d^{-1}, but consistently low nitrification rates, from undetectable up to 2 mg NO_3-N kg^{-1} d^{-1} (Carmosini et al, 2002; Westbrook et al., 2004).

The primary objective of this project was to measure the soil-atmosphere exchange of CH_4 and N_2O in Saskatchewan's three most common boreal forest stands, while concurrently studying some possible environmental controls on emissions. In addition, insight into N-cycling and N_2O flux was obtained by measuring the gross mineralization and nitrification rates in a trembling aspen stand and determining whether nitrification or denitrification was the primary source of N_2O emissions.

3.2 Materials and Methods

3.2.1 Study area

The study has three sampling sites, spanning three mature forest stands: trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* [Mill.] B.S.P.) and jack pine (*Pinus banksiana* Lamb.). These sites were based at previously established locations of the BERMS (Boreal Ecosystem Research and Monitoring Sites) project, in the mid-boreal upland ecoregion of central Saskatchewan (Figure 3). This area has the following annual averages (from Waskesiu, SK): 0.4°C air temperature, 467 mm of rainfall and 1052 growing degree days (Fluxnet-Canada, 2007). Note that 2006 and 2007 were two of the highest years for precipitation in the last decade.

The following site data is provided by Fluxnet-Canada (2007), and the Latin names are from Beckingham et al. (1996). The trembling aspen site (OTA) has a predominantly trembling aspen canopy with a few balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* [L.] Mill.) trees. The trembling aspen trees are, on average, 21 m high and 1- to 5-m apart. The thick understory is largely beaked hazel (*Corylus cornuta* Marsh.), with a variety of other common shrubs and forbs (Section 2.2). The hazel canopy varies from 1- to 3-m high. The black spruce (OBS) site is largely made up of black spruce, with a significant amount (approximately 15%) of tamarack (*Larix laricina* [Du Roi] K. Koch). The understory is mostly Labrador tea (*Ledum glandulosum* Nutt.; *Ledum groenladicum* Oeder) with a variety of mosses (*Sphagnum spp.*). The jack pine site (OJP) is an open stand of pine with several clusters of green alder (*Alnus crispa* [Ait.] Pursh) and reindeer lichen (*Cladina spp.*) covering the forest floor. Site information, including soil and water physical and chemical characteristics are included in Table 3.

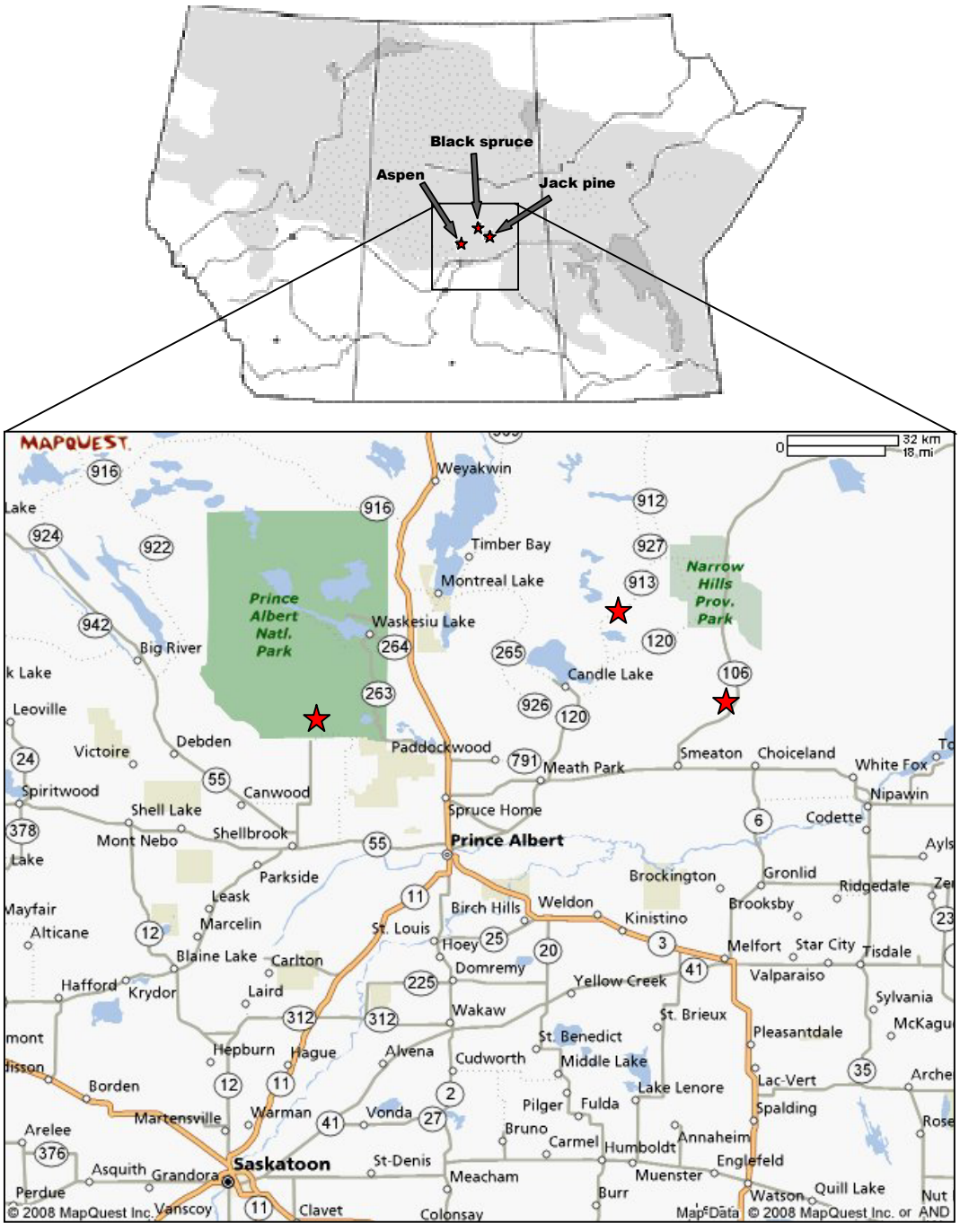


Figure 3. A map of the showing the three sampling locations, all of which are located in the mid-boreal upland ecoregion of Saskatchewan (adapted from Balland et al., 2006 and MapQuest, 2008).

Table 3. Site and soil information for three sampling sites located within different boreal forest stands (jack pine, black spruce and trembling aspen) in the mid-boreal ecoregion of Saskatchewan. Soil information is the average and standard deviation (in brackets) of twenty measurements of the 0- to 15-cm depth, along transects at each site.

Parameter	Forest stand		
	Jack Pine (OJP)	Black Spruce (OBS)	Aspen (OTA)
Site[1]			
Latitude (° N)	53.92	53.99	53.63
Longitude (° W)	104.69	105.12	106.20
Elevation (m)	579	629	601
Year established	1914	1894	1920
Average 2006 air temp. (^{o}C)	1.67	0.82	1.76
Total 2006 precip. (mm)	618	598	625
Average 2007 air temp. (^{o}C)	-1.24	-0.53	0.62
Total 2007 precip. (mm)	569	484	548
Soil			
Classification	Orthic Eutric Brunisol	Peaty-phase Gleysol	Orthic Gray Luvisol
Moss depth (cm)	-	13.9 (5.3)	-
LFH depth (cm)	3.5 (1.2)	11.7 (3.8)	8.4 (1.6)
Organic carbon (%)	0.60 (0.35)	0.74 (0.45)	0.82 (0.30)
pH	5.1 (0.3)	6.5 (0.4)	5.6 (0.4)
Density (g cm^{-3})	1.25 (0.06)	0.96 (0.24)	1.17 (0.23)
Sand content (%)	91.7 (3.7)	71.1 (8.4)	48.6 (12.5)
Silt content (%)	7.3 (3.2)	25.8 (7.5)	44.7 (10.9)
Clay content (%)	1.1 (0.7)	3.1 (1.3)	6.7 (2.1)
Water[2]			
pH	6.6	6.5 (0.3)	6.1 (0.4)
EC (µs cm^{-1})	0.13	0.19 (0.10)	0.13 (0.01)
Ca^{2+} (mg L^{-1})	16.1	20.4 (11.2)	11.3 (0.9)
Mg^{2+} (mg L^{-1})	4.9	7.8 (4.5)	3.6 (0.7)
Na^{2+} (mg L^{-1})	0.30	1.0 (0.4)	5.4 (10.6)
K^{+} (mg L^{-1})	0.68	0.38 (0.25)	14.7 (5.7)
Cl^{-} (mg L^{-1})	1.4	2.7 (0.9)	5.5 (2.6)
SO_4^{-} (mg L^{-1})	9.1	22.0 (13.6)	38.4 (11.4)

[1]Information was taken from Fluxnet-Canada (2007).
[2]OJP data are taken from a single wetland approximately 1 km from the actual transect; OBS and OTA data are averages (and standard deviations) from the four depressions along each transect.

3.2.2 Gas sampling procedure

A transect of twenty chambers spaced approximately 10 m apart was established at each site during the fall of 2005; these were used to monitor gas exchange during the summers of 2006 and 2007. The transects were chosen to cover the greatest amount of topographic variability at each site, as well as any noticeable changes in vegetation. At the OJP site, the transect covered an elevation change of approximately 2 m and had sampling locations in dry soils dominated by lichens and slightly moister areas supporting the growth of sphagnum. The OBS transect was divided into two ten-point transects, one in a dense part of the fen and the other in an area where the stand was slightly more open; each transect had eight sampling points in mossy hummocks and two in small depressions that held water for part of the season each year. The transect at OTA passed through, or near, four ephemeral wetlands; of these, two maintained standing water throughout the two years of the study, while the others dried up each summer.

Soil CH_4 and N_2O emissions were measured using chambers. The two-piece, closed, vented chambers were constructed from aluminum and consisted of a circular base and a chamber sealed together with a foam ring. The bases were inserted 3 cm into the soil and fixed using 20-cm spikes in the fall of 2005, where they remained throughout the duration of the study. At the OBS site, the bases were extended by wrapping 61 x 20-cm metal sheets around the bases and attaching them with rivets; this allowed the bases to pass through the moss and peat layers and reach the mineral soil. The chambers had a headspace of 1.87 L and covered a surface area of 0.02 m^2. In flooded areas, open water chambers were used to measure gas emissions. These chambers were a similar design, but constructed of heavy plastic and affixed to rods that were inserted into the soil. During sampling, the chambers were lowered down the rod until they were 3- to 5- cm into the water. These chambers had a headspace of 10.76 L and covered a surface area of 0.06 m^2. Docks were installed in wet regions of the OTA site to minimize disturbance of the water and riparian areas when doing open water sampling. Small wooden platforms were placed at each transect location at the OBS site, to minimize the disturbance of the moss.

At each site, regular measurements of soil N_2O and CH_4 efflux were taken from the chambers along the transects. In order to ascertain flux rates, gas was sampled four times over twenty-four minutes, in eight minute intervals. Ambient air samples were also collected once during each interval. Gas samples were taken using a 20-mL syringe and injected into 12-mL Labco Exetainer® (Labco Limited, UK) evacuated tubes. Once they were returned to the lab, the samples were stored at < 4°C until analysis could be completed. Gas measurements occurred weekly throughout the summer of 2006 (May-August) and biweekly throughout the summer of 2007. Biweekly sampling continued through September and October during both years of the study.

During or immediately following the gas sampling each week, soil temperature and moisture readings were taken. Adjacent to each transect chamber, temperature was measured using thermocouples at 5- and 20- cm below the soil surface; the thermocouple reader was also used to measure ambient air temperatures above the surface, at each point. The thermocouples were made of twisted copper and constantan (45% Ni and 55% Cu) wire pairs; they were read using a Barnant DuaLogR™ thermocouple reader (Barnant Company, Barrington, IL). During 2006, moisture was measured 15 cm below the soil surface primarily using a TDR100 coupled to a CR10X datalogger (Campbell Scientific Canada Corp., Edmonton, AB) and a 2-pronged, 15 cm probe. However, when this system failed near the end of August, gravimetric sampling was substituted. Gravimetric measurements were continued during 2007 for the sake of continuity.

On July 26th 2006, three soil-sampling locations were selected at each site. The locations were approximately equidistant along the length of the transect, in order to capture the maximum possible variation at the site. At each site, three pits approximately 1 m x 1 m were dug and used to describe the soil profiles. On the same date, samples were taken from each transect point and returned to the lab in order to measure the depth of the LFH, soil bulk density, organic carbon, pH and particle size (methods described in Section 3.2.3) (Table 1). At the end of October 2006, six 1.2 m PVC piezometers were installed at each site, arranged in groups of two at locations along the transects where it appeared possible for water to remain close to the soil surface throughout the year. These were used to monitor the water table once the

standing water dried down. During the summer of 2007, water samples were taken from each area of standing water along the transects (at OJP it was an area approximately 1 km from the transect) and analyzed for water chemistry (Table 3).

At the beginning of the 2007 season, six chambers were installed at OJP and OBS, in areas along the transect that had all of the LFH removed. These were measured concurrently with the regular transect in order to ascertain whether the LFH layer significantly affected gas emissions. No significant differences were found, so this part of the experiment will not be discussed further in this paper. At OTA, additional chambers were added to two lower slope areas in an attempt to capture a more detailed picture of the initiation and cessation of the emissions in these areas. Unfortunately, these areas did not emit more than background levels of the two gases, so no significant differences were seen. The three sites were always sampled over two days, starting with OJP and OBS on day one, and then OTA on day two; this minimized the driving time required. In order to determine whether the gas emission results were being biased by consistently sampling each site at a different time of day, one 12-hour sampling date was completed at each site. These occurred on the 4th, 5th and 6th of July, 2007, since the previous year had indicated that this should be a period during which high emissions occurred. On these days, the transects were sampled four times, at 6:30, 10:00, 13:30 and 17:00, with the exception of the OJP site which was sampled at 6:30, 10:00 and 15:30.

3.2.3 Soil and gas analyses

Organic carbon was measured by combustion at 840°C in a LECO® CR-12 Carbon System (Leco Corporation, St. Joseph, MI). Soil particle size was determined using a Horiba LA950 Laser Diffraction Particle Size Analyzer; since the organic carbon was low, samples were added dry for the particle size analysis, after being air-dried, ground using a flail-grinder and sieved to <2 mm. The pH was analyzed using an Accumet AP85 portable pH/Conductivity meter on a 1:1 (by weight) solution of soil and water. The bulk density was determined by collecting, drying and weighing the top 0- to 15-cm of soil, sampled using a density sampler with a radius of 4 cm. Density was used to calculate water-filled pore space (WFPS) using the equation:

$$WFPS = (SM*BD)/(1-(BD/PD)) \quad (3.1)$$

SM = soil moisture (g g^{-1})
BD = bulk density (g cm^{-3})
PD = particle density (2.65 g cm^{-3})

Gas samples were analyzed using a Varian CP-3800 GC (Varian Canada Inc., Mississauga, ON) with dual electron capture detectors (ECD's) for N_2O and a flame ionization detector (FID) for CH_4. N_2O separations were carried out by Poraplot Q fused silica columns (10 m length x 0.32 mm diameter, film thickness = 0.32 μm); operating conditions for the GC were: 70°C injector temperature, 35°C oven temperature and 370°C detector temperature. CH_4 separations used a Porapak Q8 column (3.7 m length x 0.3 cm diameter, film thickness = 2 mm); operating conditions for the GC were: 70°C injector temperature, 50-200°C oven temperature and 200°C detector temperature. The carrier gas was ultra-high purity He (7.9 and 14.4 mL min^{-1} for ECD's, 40 mL min^{-1} for FID) with P5 (95:5 v/v Ar:CH_4 mix) as the make-up gas for the ECD's (10 and 12.0 mL min^{-1}). Samples (N_2O:300 μL, CH_4:900 μL) were introduced using a CombiPAL auto-sampler (CTC Analytics AG, Switzerland) with on-column injection and a split ratio of 10:1 for the ECD's. Data processing was performed using the Varian Star Chromatography Workstation (ver. 6.2) software. Internal calibration curves were acquired by applying linear least squares regression to the gas concentration versus peak area data; gas concentrations in the samples were then calculated from the regression equations.

Ambient air samples were included in each analytical run, and used to check precision, correct for detector drift and calculate the minimum detectable concentration difference (MDCD). The MDCD was calculated from the average of pairs of ambient samples using the following equation:

$$MDCD = \mu_{\text{pair diff}} + (2\sigma_{\text{pair diff}}). \quad (3.2)$$

μ = average difference between sample pairs
σ = standard deviation between sample pairs

When calculating the gas flux, the MDCD was used to determine if the samples for each time step were significantly different from t_0; if the concentration difference between t_0 and each time step was < MDCD, they were not considered different. If they were significantly different, the four time steps were used to calculate gas flux by fitting a polynomial equation to the curve they generated. The flux was calculated as the first derivative of the second-order polynomial equation ($y = ax^2 + bx + c$) used to describe the relationship between concentration and time. The MDCD and flux calculation are described in greater detail by Yates et al. (2006).

The cumulative annual emissions for each site were calculated using forward multiplication. Emissions were assumed to be constant throughout the day and between sampling dates, so that the flux rate was simply multiplied by the time that elapsed between each measurement. In order to use the "per year" designation, it was assumed that no emissions occurred outside of the sampling season (May to October) each year.

3.2.4 Isotope sampling procedure

In addition to monitoring gas flux, a more intensive study of nitrogen cycling was included to examine the source of N_2O emissions. This was carried out only at OTA, as the site conditions (Section 3.2.1) indicated it would likely be the most productive of the three sites. On May 31st, July 19th and August 23rd 2006, and June 1st, July 21st and August 30th 2007, the relative contribution of nitrification and denitrification to N_2O emissions was measured at every other point along the OTA transect, using a stable isotope (^{15}N) technique.

In 2006, thirty intact soil cores (3 from each sampled transect point) were taken from OTA; cores were 15 cm deep with a volume of 294.5 cm^3. Labeled N (^{15}N) was injected into twenty of the cores (two from each set) in the form of $K^{15}NO_3$; injections were done using an 18-gauge side-port spinal needle (Popper and Sons). The cores were labeled with six, 2-mL injections of 3.5 ppm N solution, which added 42 µg of N (98% ^{15}N) to each core. The concentrations of the solutions were chosen to facilitate the homogeneity of the label in the core (maximum volume) while not increasing the gravimetric soil moisture content to more than 40% (average based on earlier field

measurements). Because of the very low levels of background NO_3^- in the boreal forest, the added N increased the NO_3^- pool by about 42% in each core.

Of each pair of labeled soil cores, one was extruded and extracted with 2M KCl within an hour after injection, while the other - capped only on the bottom - was sealed in a Mason jar and incubated in the field for twenty-four hours. The third core from each location (unlabelled) was also incubated to provide a background measurement of gas emissions (these numbers were used to ascertain whether there was an increase in emissions due to the method used). The jars were incubated in a hole and covered with the LFH layer, to simulate the temperature conditions that they would normally be subject to. The lids of the jars had septa fitted into them; before and after the incubation period, gas was sampled from the jars using a 20-mL syringe and injected into 12-mL Labco Exetainer® (Labco Limited, UK) evacuated tubes. After the first gas sample (before the 24-hour incubation) the lids were removed briefly to allow the headspace in the jars to be refreshed. After 24 hours, the gas from the jars was sampled a second time, and then the incubated cores were extruded and extracted with 2M KCl. The extracts from each pair of labeled cores were meant to be used to measure gross nitrification, but were unsuccessful due to contamination in the soil extracts; this source of error was remedied by the next summer.

The methodology in 2007 was the same as that used in 2006, but included measurements of gross mineralization and gross nitrification in the soil cores via the isotope dilution method (Davidson et al., 1991). This involved sampling five soil cores from each site (50 total) and injecting two pairs of cores: one pair for mineralization and one pair for nitrification. The cores used for nitrification were injected with $K^{15}NO_3$ (42 µg N per core with 98% enrichment) and those for mineralization were injected with $(^{15}NH_4)_2SO_4$ (336 µg N per core with 98% enrichment). After they were labeled, one of each pair was immediately extruded and a sub-sample extracted using 2M KCl. The remaining two cores, together with the background cores, were sealed into Mason jars, gas sampled, and incubated as previously described. Once the incubation was complete and the second set of gas samples taken, the incubated cores were extruded and extracted on-site. The extract containers and soil bags were placed in coolers filled with

ice until they could be returned to the lab (approximately 4 hours after extractions were completed on Day 2).

3.2.5 Isotope analyses

Soil samples for the ^{15}N experiment were extracted with Whatman #2 filter paper. Total inorganic N was determined by analyzing the extracts for NO_3^- and NH_4^+ colorimetrically using a Technicon AutoAnalyzer (Technicon Industrial Systems, 1978). Extracts were then analyzed for $^{15}NH_4$ and $^{15}NO_3$ by NH_3 diffusion onto polytetrafluoroethylene-encased acid traps (Stark and Hart, 1996). The $^{15}NH_4$ and $^{15}NO_3$ on the diffusion disks were determined at the University of Saskatchewan using a RoboPrep CN elemental analyzer coupled to a continuous flow TracerMass mass spectrometer (MS) (Europa Scientific, SerCon Ltd., Crewe, UK); the combustion tube was at 1000ºC and the reduction tube was at 600ºC. Gross mineralization and nitrification were calculated as the difference in the ratio of ^{14}N to ^{15}N between the t_0 and t_{24} soil cores (Hart et al., 1994). Gas samples for the ^{15}N experiment were analyzed at the UC Davis Stable Isotope facility using a SerCon CryoPrep trace gas concentration system interfaced to a PDZ Europa 20-20 isotope ratio MS (Sercon Ltd., Cheshire, UK). The MS measured total N_2 and N_2O, as well as $^{15}N_2$ ($^{29}N_2$, $^{30}N_2$) and $^{15}N_2O$ ($^{45}N_2O$, $^{46}N_2O$). These were used to determine the role of denitrification in N_2O emissions using the following equation from Stevens et al. (1997):

$$d = (a_m - a_n)/(a_d - a_n) \qquad (3.3)$$

d= proportion of N_2O from denitrification

a_m= enrichment of N_2O mixture ($^{15}N_2O/[^{14}N_2O+^{15}N_2O]$)

a_n= enrichment of NH_4^+ pool ($^{15}NH_4^+/[^{14}NH_4^++^{15}NH_4^+]$)

a_d= enrichment of NO_3^- pool ($^{15}NO_3^-/[^{14}NO_3^-+^{15}NO_3^-]$)

The relative importance of nitrification-related processes was calculated as the difference between d and 100%.

3.3 Results

3.3.1 Methane

The seasonal CH_4 emissions for each site are shown in Figures 4 through 6 (the 20 cm soil temperatures are not shown since they exhibited the same pattern as the 5 cm values). At OJP and OBS there is no clear seasonal pattern in either year, although the OJP soil is consistently a sink (Figure 4) while OBS is more variable (Figure 5). The lack of a seasonal pattern was emphasized by the poor correlations between emissions and temperatures at the sites. Using a significance of $p = 0.05$, there were no correlations with air or soil temperature at either of OJP or OBS. As shown in Figure 7, the WFPS over the season was significant at OJP in 2006 ($r = 0.64$; $p = 0.02$), but not in 2007 ($r = 0.28$; $p = 0.46$). There were no correlations with WFPS at OBS.

Unlike the other two sites, the seasonal emissions at OTA were significantly correlated with soil temperature, although not with air temperature. The 2006 and 2007 correlations with the temperature 5 cm below the soil surface ($r = 0.73$ and $p = 0.001$ in 2006; $r = 0.60$ and $p = 0.03$ in 2007) are shown in Figure 8. The 20 cm correlations are not shown, as they exhibited the same pattern as the 5 cm depth ($r = 0.68$ and $p = 0.002$ in 2006; $r = 0.59$ and $p = 0.03$ in 2007). The relationship with temperature at OTA was exhibited by the clear seasonal pattern in both years, where high CH_4 emissions occurred from late June through August (Figure 6). The high emissions extend later in 2007, possibly due to the unusually warm fall. There was also a diurnal variation in the CH_4 emissions at OTA; although sampling points that exhibited negligible emissions (the upland areas) were constant, those with elevated emissions (the depressional areas) increased from morning to afternoon and then decreased again towards evening (Figure 9). The CH_4 emissions at OTA were not correlated with WFPS in either year, although they were dependent on the presence of water. The increase in 2007 emissions in Figure 6 somewhat paralleled the temperature increase up until the middle of July, at which point they declined dramatically. This decline occurred at the same time that four of five previously-flooded sampling points dried up.

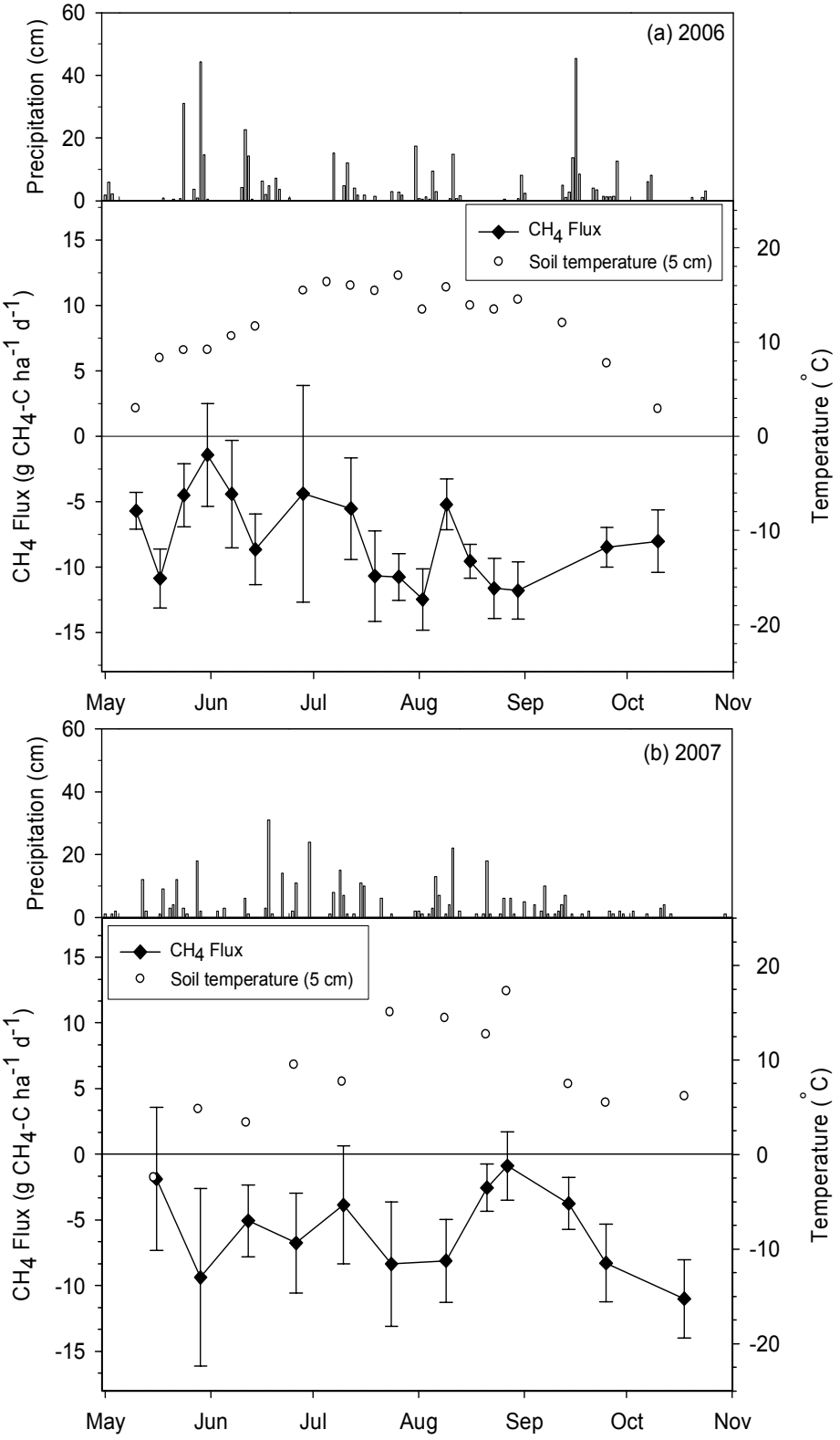


Figure 4. Old growth jack pine stand (OJP) daily methane fluxes, precipitation (Fluxnet-Canada, 2008) and temperature (5 cm below the soil surface), from the frost-free period of 2006 (4a) and 2007 (4b). Flux values were calculated by averaging the daily flux measurements from a 20-point transect; error bars show standard error.

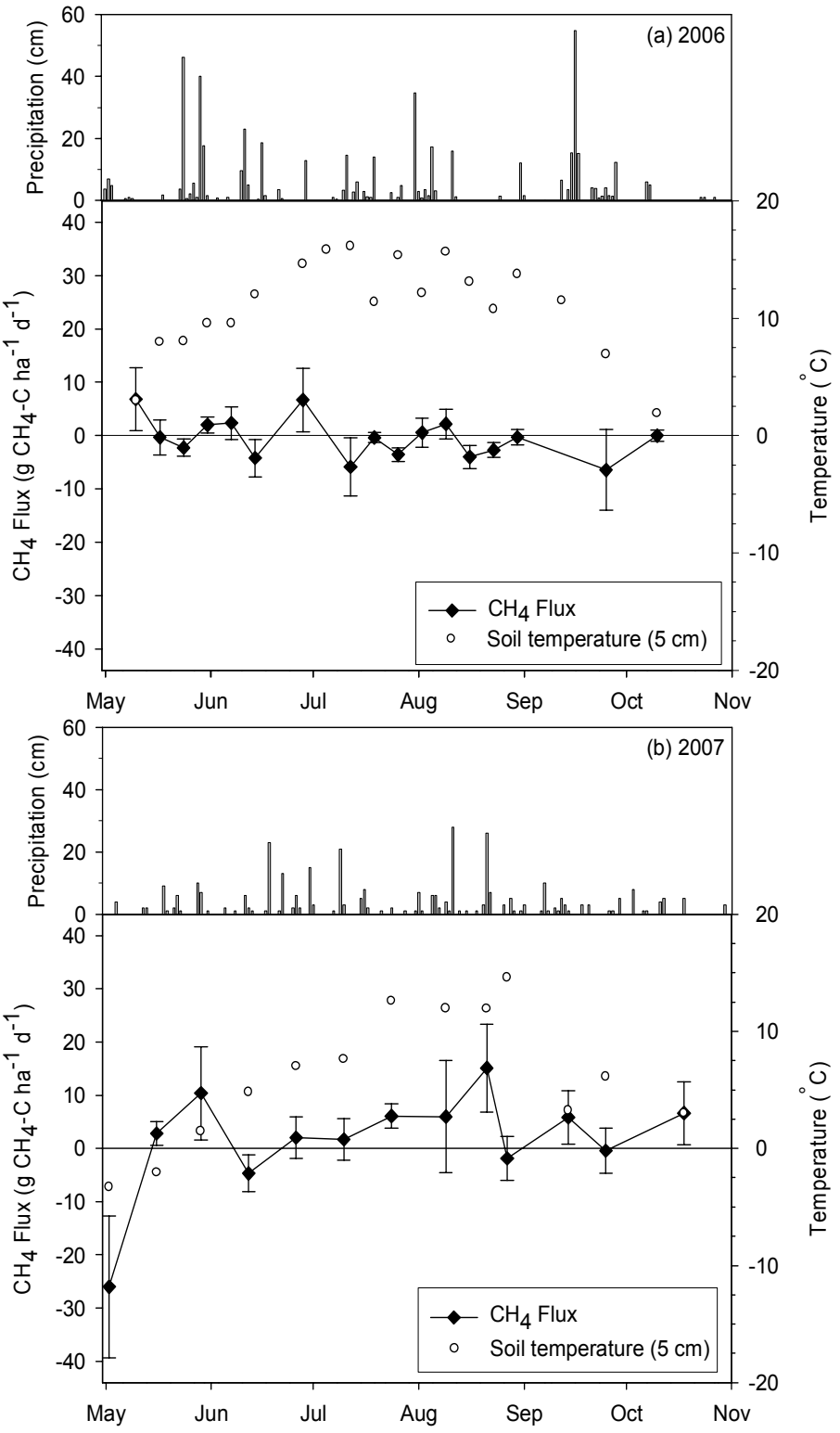


Figure 5. Old growth black spruce stand (OBS) daily methane fluxes, precipitation (Fluxnet-Canada, 2008) and temperature (5 cm below the soil surface), from the frost-free period of 2006 (5a) and 2007 (5b). Flux values were calculated by averaging the daily flux measurements from a 20-point transect; error bars show standard error.

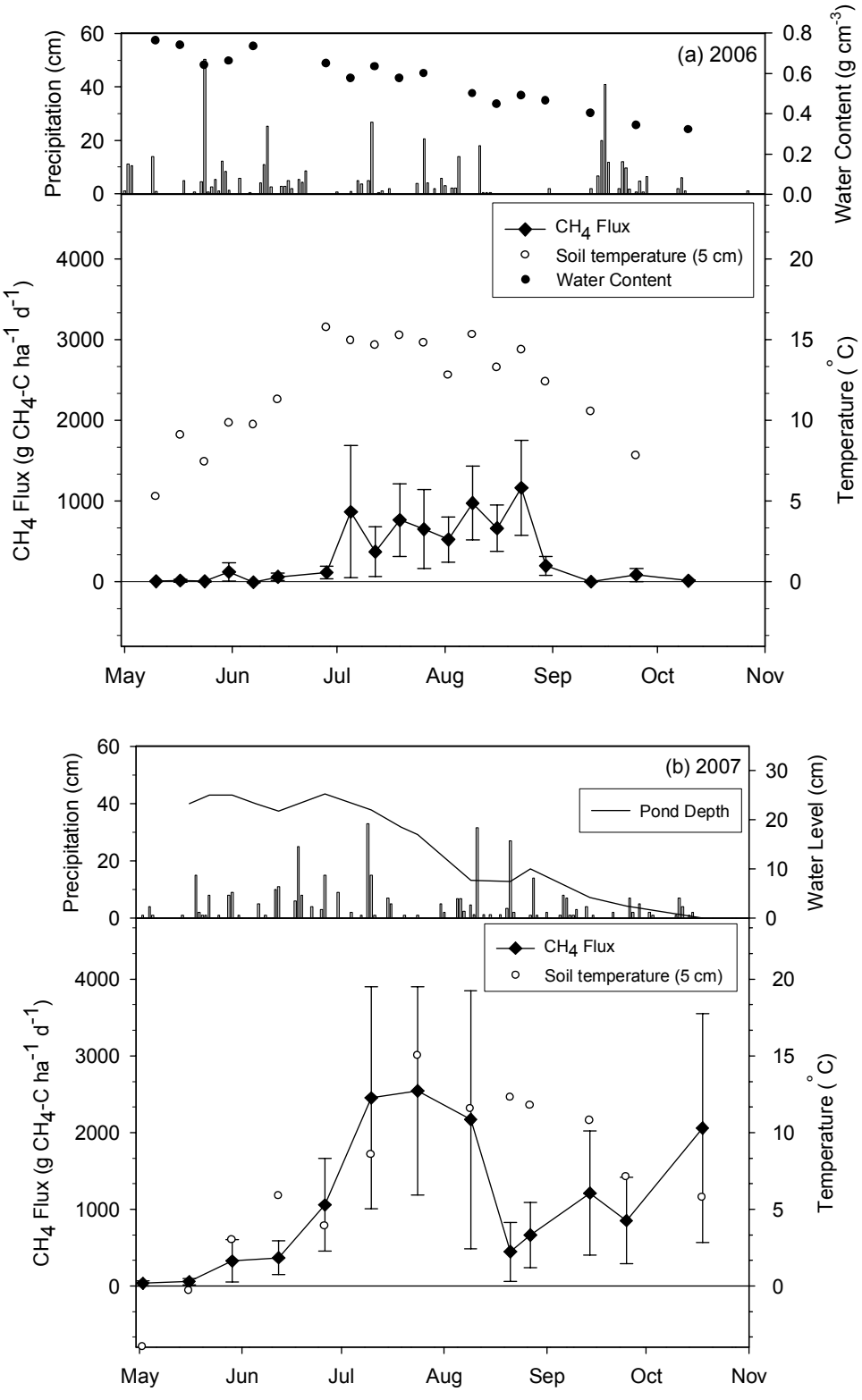
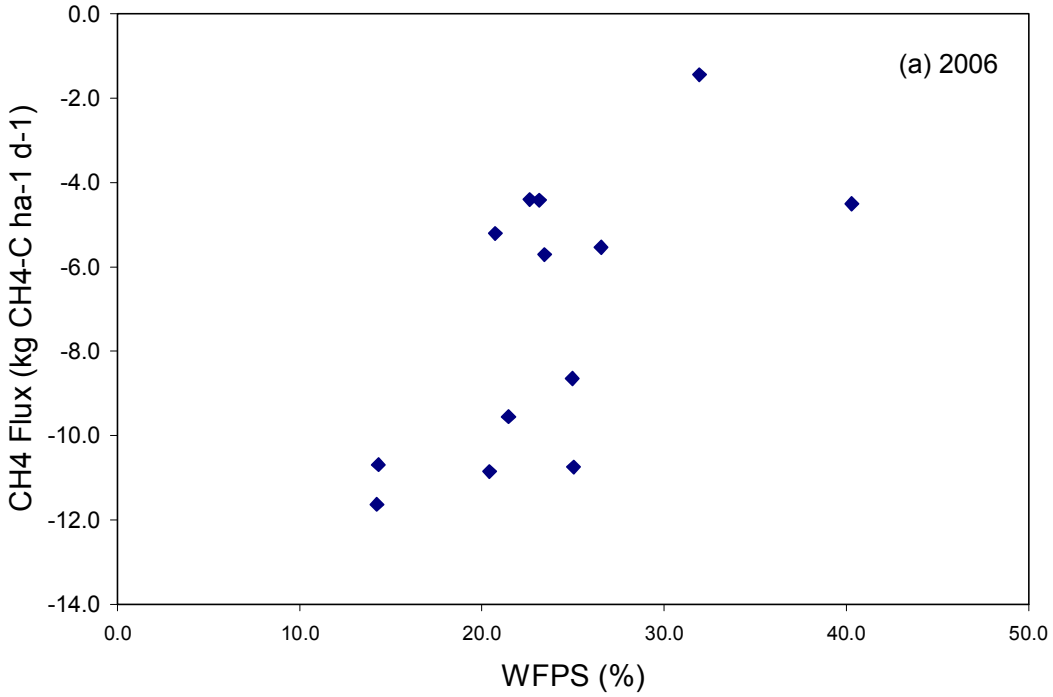


Figure 6. Old growth trembling aspen stand (OTA) daily methane fluxes, precipitation (Fluxnet-Canada, 2008), temperature (5 cm below the soil surface) and mean volumetric water content (2006)/mean pond depth (2007). Flux values were calculated regularly during the frost-free period of 2006 (6a) and 2007 (6b), by averaging the daily flux measurements from a 20-point transect; error bars show standard error.



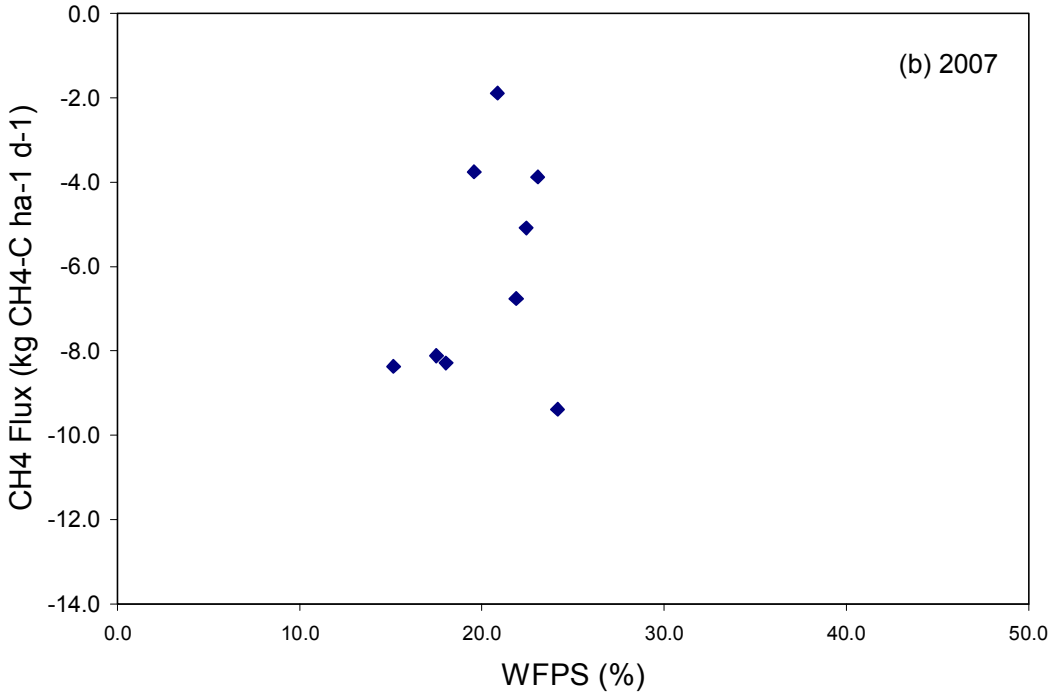
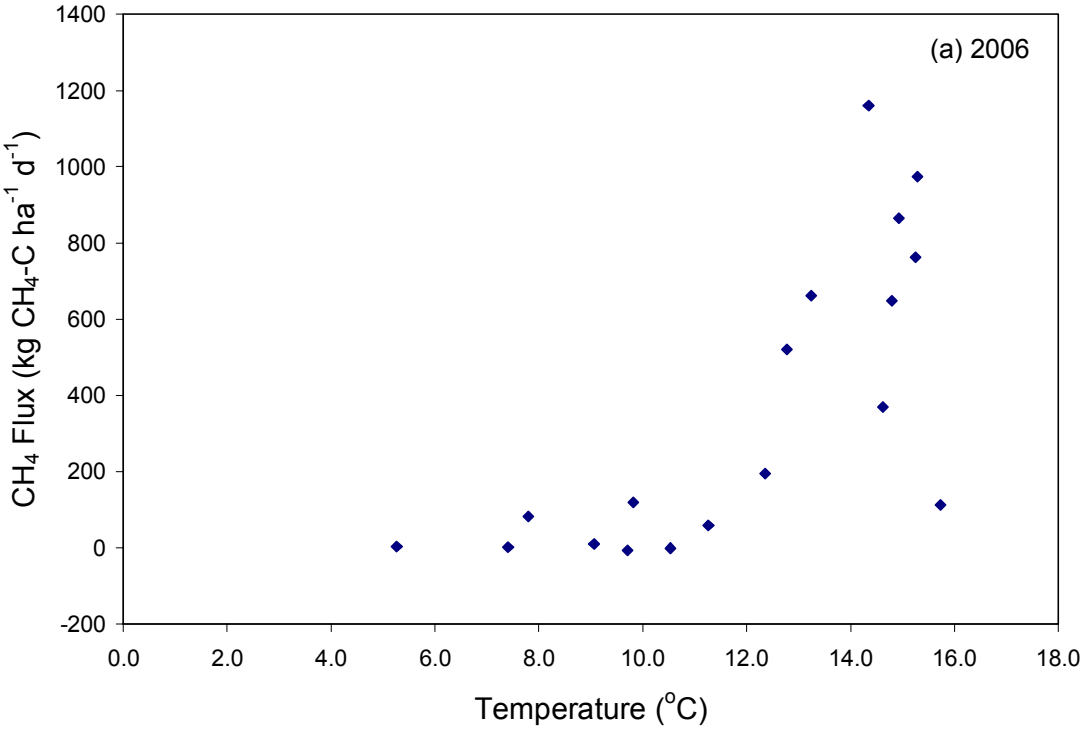


Figure 7. Old growth jack pine stand (OJP) average daily methane emissions from 20 sampling points, on 14 sampling dates in 2006 (7a) and 9 dates in 2007 (7b), plotted against the % water-filled pore space (WFPS) on each date. The two-tailed Pearson correlations were $r = 0.64$ ($p = 0.02$) in 2006 and $r = 0.28$ ($p = 0.46$) in 2007.



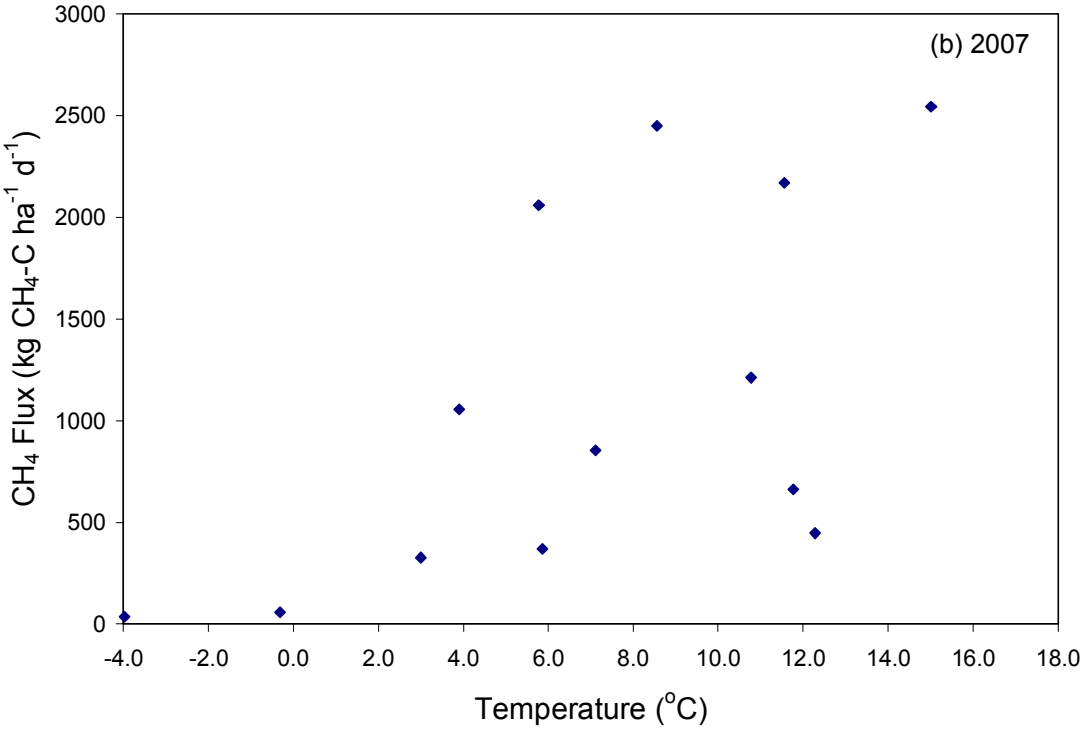


Figure 8. Old growth trembling aspen stand (OTA) average daily methane emissions from 20 sampling points, on 18 sampling dates in 2006 (8a) and 13 dates in 2007 (8b), plotted against the average soil temperature (°C) 5 cm below the soil surface on each date. The two-tailed Pearson correlations were r = 0.73 (p = 0.001) in 2006 and r = 0.60 (p = 0.03) in 2007.

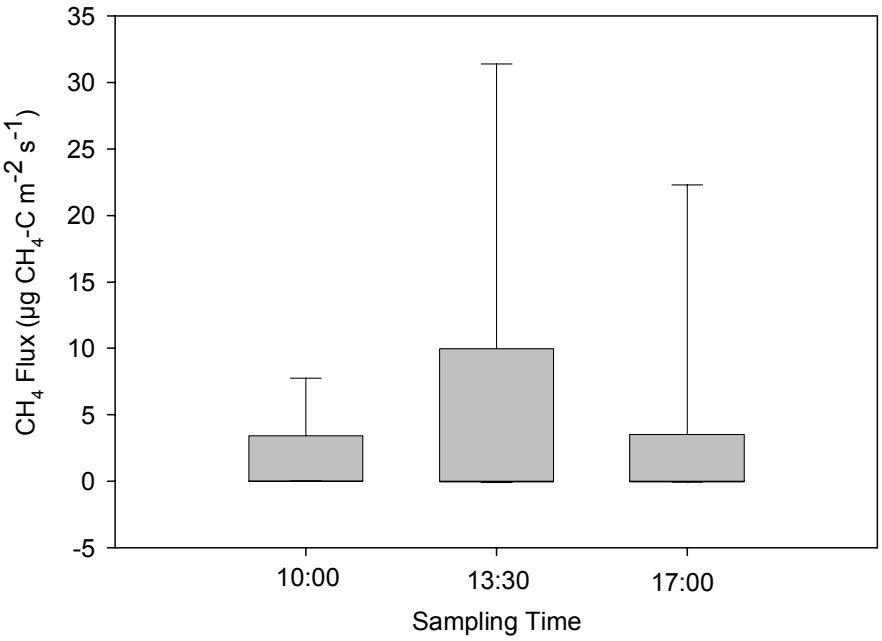


Figure 9. The range of methane emissions measured throughout the day on one-half of a 20-point transect, in an old growth trembling aspen stand on July 4th 2007.

In terms of soil properties at each transect location, the emissions from all three sites were correlated with SOC in 2006 (r = -0.60 and p = 0.01 at OJP, r = -0.53 and p = 0.02 at OBS, and r = 0.62 and p = 0.01 at OTA), but only emissions at OJP were significant at the 0.05 level in 2007 (r = -0.46; p = 0.04) (Figures 10-12). It is notable, though, that the relationships at both OJP and OTA were dependent upon a single point to make them significant. In addition to SOC, additional factors examined included particle size, pH, density, LFH thickness and soil temperature, but there were no other significant correlations at OJP or OTA. Emissions from OBS were correlated with the amount of clay in the soil in 2007 (r = -0.56; p = 0.01), but not in 2006 (r = 0.33; p = 0.17) (Figure 13). All of the relationships were quite weak, and not consistent from 2006 to 2007. This suggests that either the controlling factors changed from year to year, or the correlations themselves were coincidences rather than real relationships.

Although no topographic patterns were found at OJP or OBS, at OTA all of the high fluxes came from three of the four depressional areas (Figure 14). As shown in Figure 14, the depression at #11 was the only one which exhibited no significant emissions in either year. Although there was no explanation for the lack of emissions found within the data, there were two differences noted between this depression and the others at the site. One difference was that although it was flooded in the spring of both years, #11 was at a slightly higher position in the landscape than the other depressions and dried up more quickly in the spring. The second difference was that #11 had much less vegetation at the beginning of the study than the others. There was vegetation throughout the depression at #15 in the spring of 2006 when the study began, but the hazel understory experienced significant die-back that year - as it did at the edges of the two semi-permanently flooded wetlands - after being flooded for much of the season. The abundance of flood-intolerant vegetation suggests that these areas had not been flooded in the years immediately preceding this study. This is contrasted with the depression at #11, which had no shrubby vegetation in 2006, indicating that it may experience some flooding every year. In addition to the lack of emissions from #11, the other notable feature of Figure 14 is the lack of high emissions from the depression at #15 in 2007. Since #15 exhibited significant emissions in 2006 when it was flooded, the low emissions in 2007 were attributed to the lack of standing water that year.

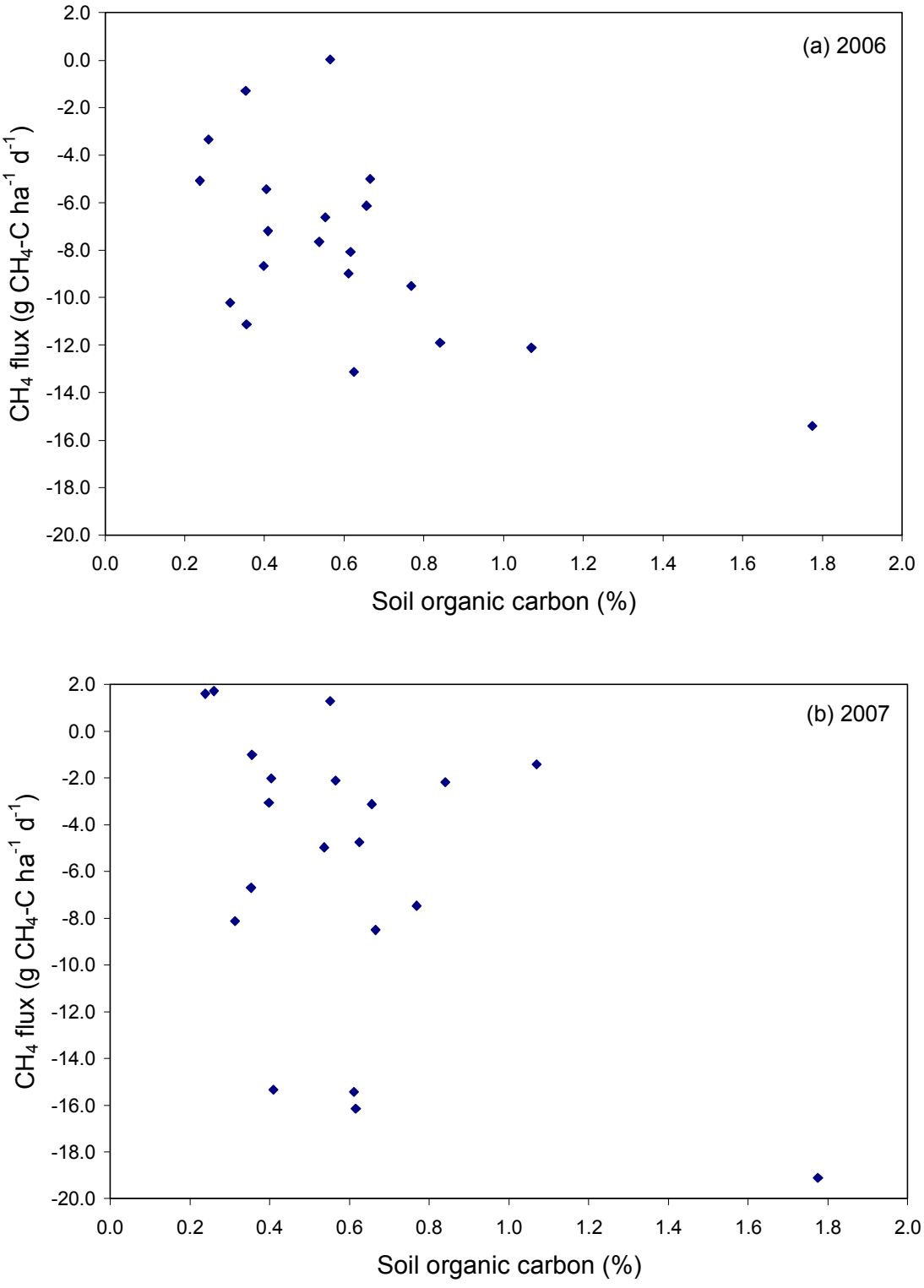


Figure 10. Old growth jack pine stand (OJP) average daily methane emissions from May to October (19 dates in 2006 and 13 dates in 2007), from 20 sampling locations in 2006 (10a) and 2007 (10b), plotted against the soil organic carbon (%) at each location. The two-tailed Pearson correlations were r = -0.60 (p = 0.01) in 2006 and r = -0.46 (p = 0.04) in 2007.

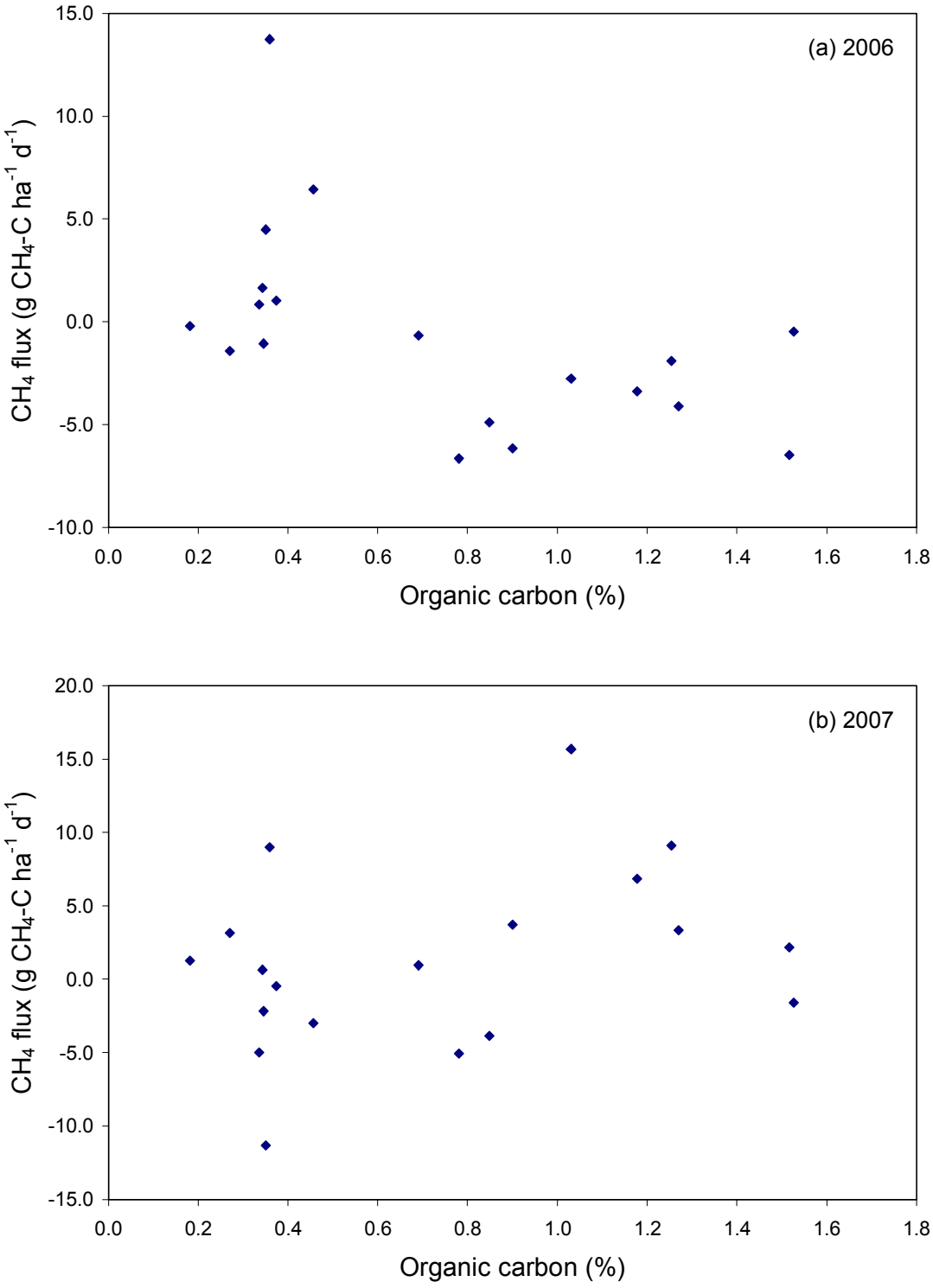


Figure 11. Old growth black spruce stand (OBS) average daily methane emissions from May to October (19 dates in 2006 and 13 dates in 2007), from 20 sampling locations in 2006 (11a) and 2007 (11b), plotted against the soil organic carbon (%) at each location. The two-tailed Pearson correlations were r = -0.54 (p = 0.02) in 2006 and r = 0.34 (p = 0.15) in 2007.

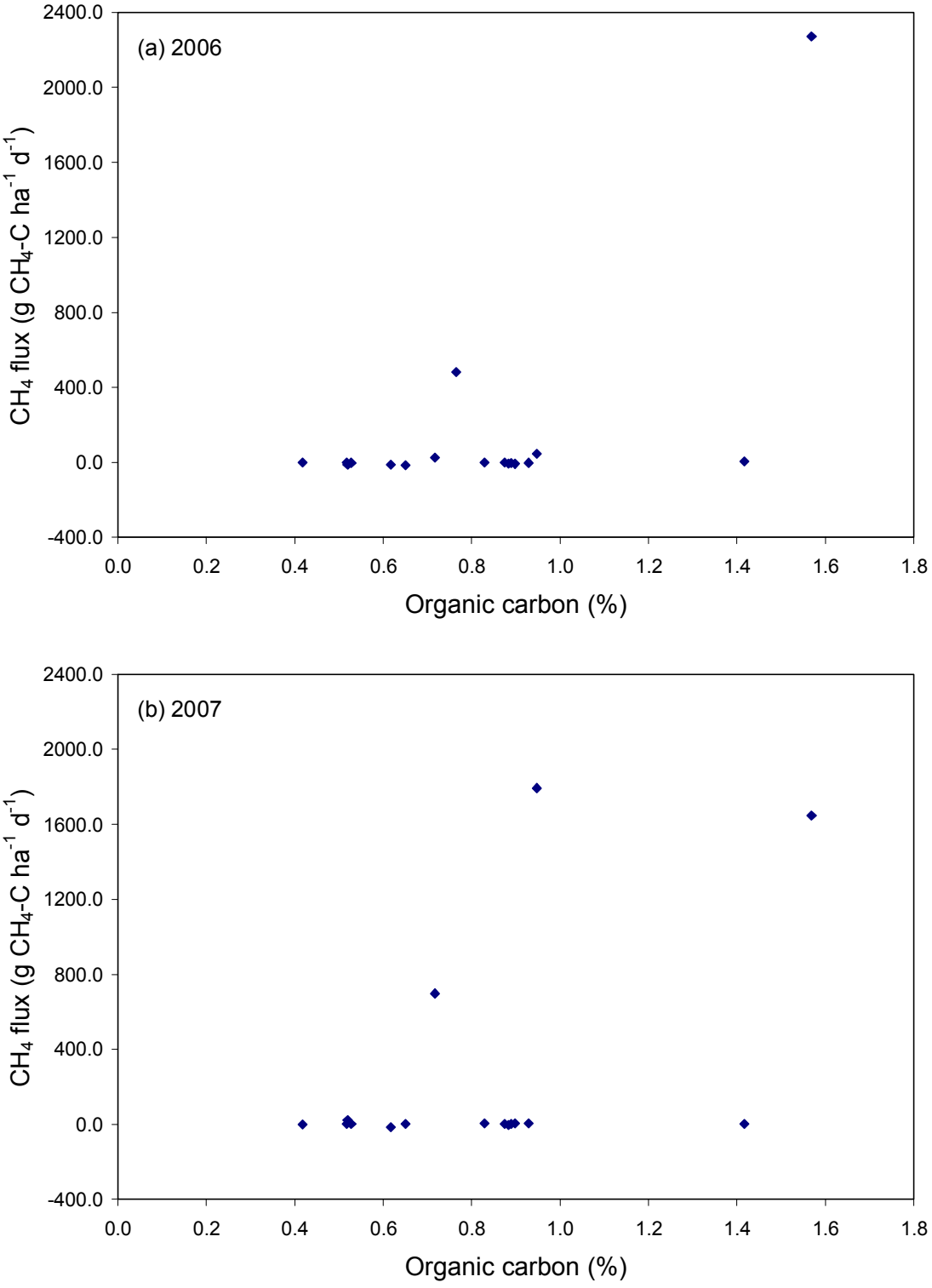


Figure 12. Old growth trembling aspen stand (OTA) average daily methane emissions from May to October (19 dates in 2006 and 13 dates in 2007), from 17 sampling locations in 2006 (12a) and 2007 (12b), plotted against the soil organic carbon (%) at each location. The two-tailed Pearson correlations were $r = 0.62$ ($p = 0.01$) in 2006 and $r = 0.10$ ($p = 0.71$) in 2007.

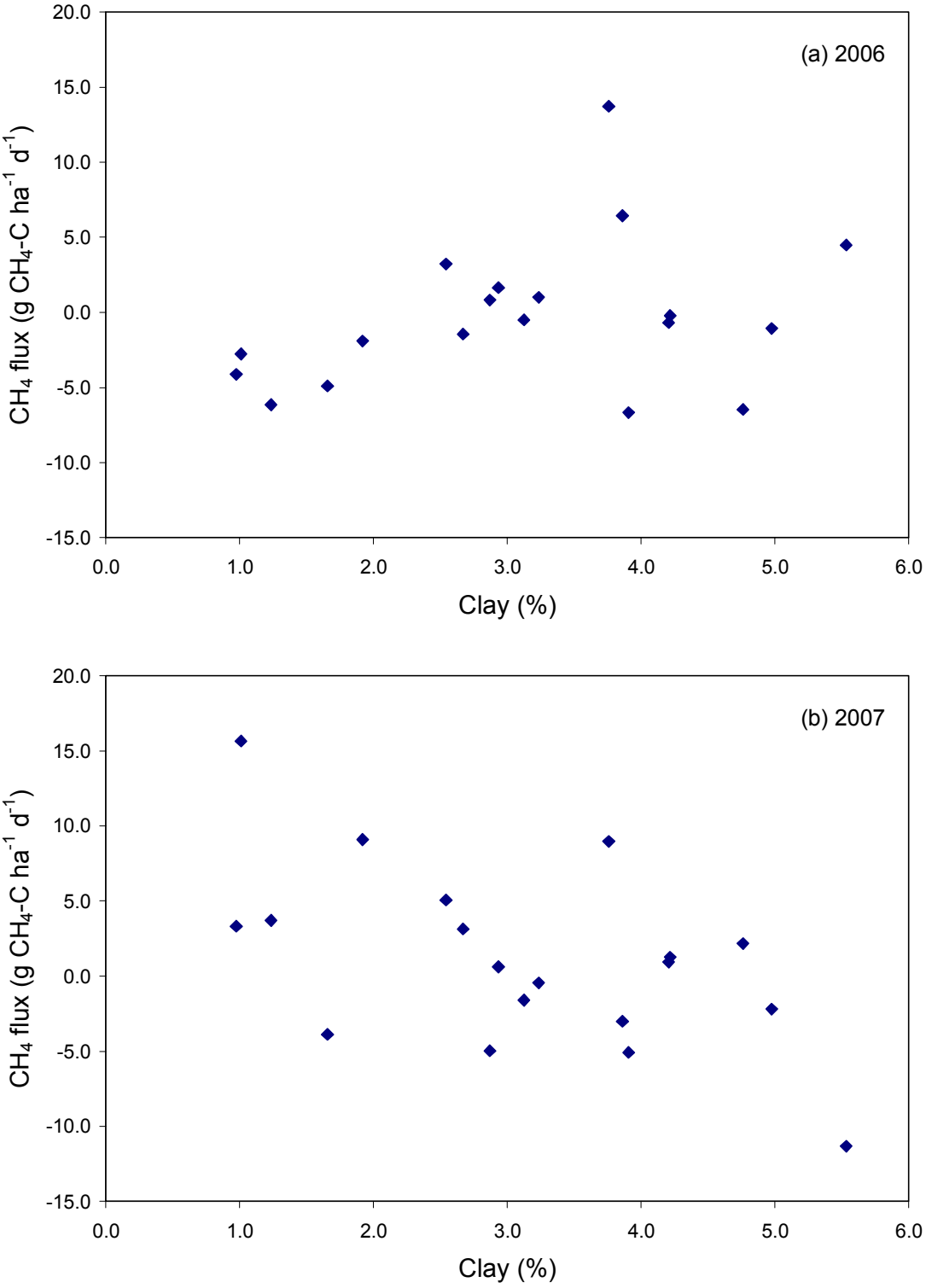


Figure 13. Old growth black spruce stand (OBS) average daily methane emissions from May to October (19 dates in 2006 and 13 dates in 2007), from 19 sampling locations in (13a) 2006 and (13b) 2007, plotted against the clay content (%) of the soil at each location. The two-tailed Pearson correlations were $r = 0.33$ ($p = 0.17$) in 2006 and $r = -0.56$ ($p = 0.01$) in 2007.

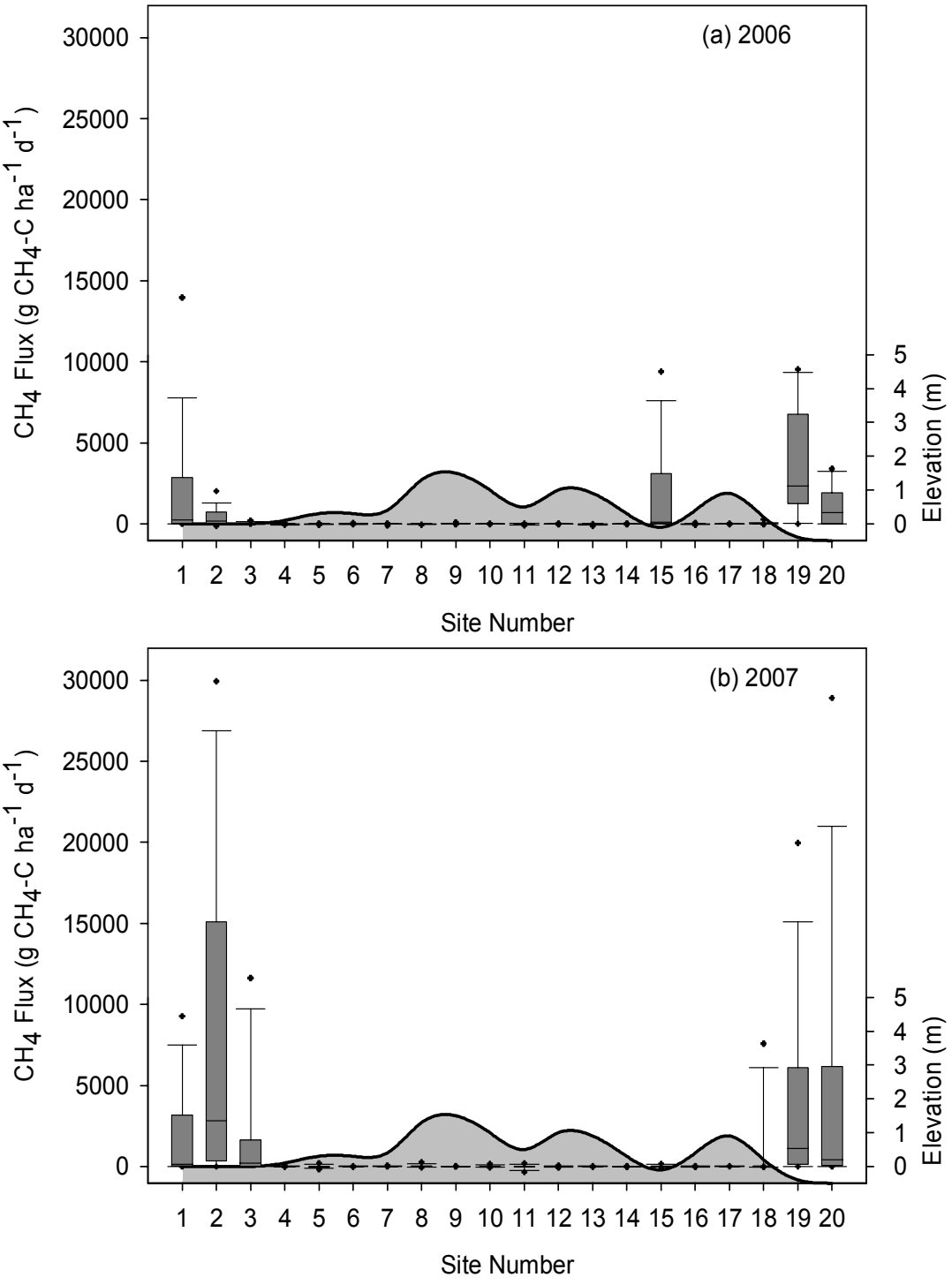


Figure 14. The range of daily methane emissions from an old growth trembling aspen stand (OTA) measured over the frost-free period of 2006 (14a) and 2007 (14b) from each location along a transect (elevation shown by the solid black line). In 2006, emissions were measured weekly from May to August and biweekly in September and October (boxplot N=19). In 2007, emissions were measured biweekly from May to October (boxplot N=13). Note that boxplots are shown for each site along the transect, but the ranges are extremely small except in depressional areas.

In 2006, the OJP and OBS sites were both cumulatively slight sinks of CH_4 (-1.23 kg CH_4-C ha^{-1} $yr^{-1}$and -0.17 kg CH_4-C ha^{-1} yr^{-1} respectively), whereas OTA was a net source (46.7 kg CH_4-C ha^{-1} yr^{-1}). The following year, the OJP site was a slight sink (-0.95 kg CH_4-C ha^{-1} yr^{-1}), the OBS site was a slight source (0.45 kg CH_4-C ha^{-1} yr^{-1}) and the OTA site was a considerable source (196.0 kg CH_4-C ha^{-1} yr^{-1}). Note that since they were usually sampled in early afternoon, the trembling aspen emissions may have been overestimated (Figure 9). This information is summarized in Table 4.

3.3.2 Nitrous oxide

The seasonal N_2O emissions for each site are shown in Figures 15 through 17. The average site emissions over the frost-free period were not correlated with any of the climatic variables measured. Assessing the graphs visually does indicate that both OJP and OBS may have exhibited a seasonal pattern, in that they experienced a flush of activity in mid-June through July during both years. At OTA, a short period of N_2O emissions appeared in August during both years, as well as a flush of activity in mid-June through July in 2007. Despite the possible seasonality in their pattern, though, the consistently low emissions in both years place these sites in the category of background emission types and not seasonal emission types (as defined by Brumme et al., 1999).

In terms of soil properties, the N_2O emissions from OJP and OBS were not significantly correlated with particle size, SOC, pH, density, LFH thickness or soil temperature. There was one significant correlation at OTA. Although the 2006 N_2O emissions were not significant (r = -0.24; p = 0.36), emissions in 2007 were positively correlated with the % clay in the soil (r = 0.60; p = 0.01) (Figure 18). Unlike the CH_4 emissions, there were no visual differences in N_2O emissions between the sampling points along the transect at OTA (Figure 19), OJP or OBS, that would indicate the presence of a topographical control.

All three sites had very low cumulative N_2O emissions. In 2006, emissions ranged from 0.05 kg N_2O-N ha^{-1} yr^{-1} at OJP, to 0.12 and 0.13 kg N_2O-N ha^{-1} yr^{-1} at OTA and OBS respectively. In 2007, OBS emissions became a slight sink (-0.02 kg N_2O-N ha^{-1} yr^{-1}), while the others remained similar, measuring 0.08 and 0.14 kg N_2O-N ha^{-1} yr^{-1} for OJP and OTA respectively. This information is summarized in Table 4.

Table 4. Cumulative methane (CH_4) and nitrous oxide (N_2O) emissions from three boreal forest stands in 2006 and 2007. Measurements were taken from a jack pine (OJP), black spruce (OBS) and trembling aspen (OTA) stand from May to October each year, and activity was assumed to be negligible for the rest of the year.

Site	Year	CH_4 Emissions	N_2O Emissions
		(kg CH_4-C ha^{-1} yr^{-1})	(kg N_2O-N ha^{-1} yr^{-1})
OJP	2006	-1.23	0.05
	2007	-0.95	0.08
OBS	2006	-0.17	0.13
	2007	0.45	-0.02
OTA	2006	46.7	0.12
	2007	196.0	0.14

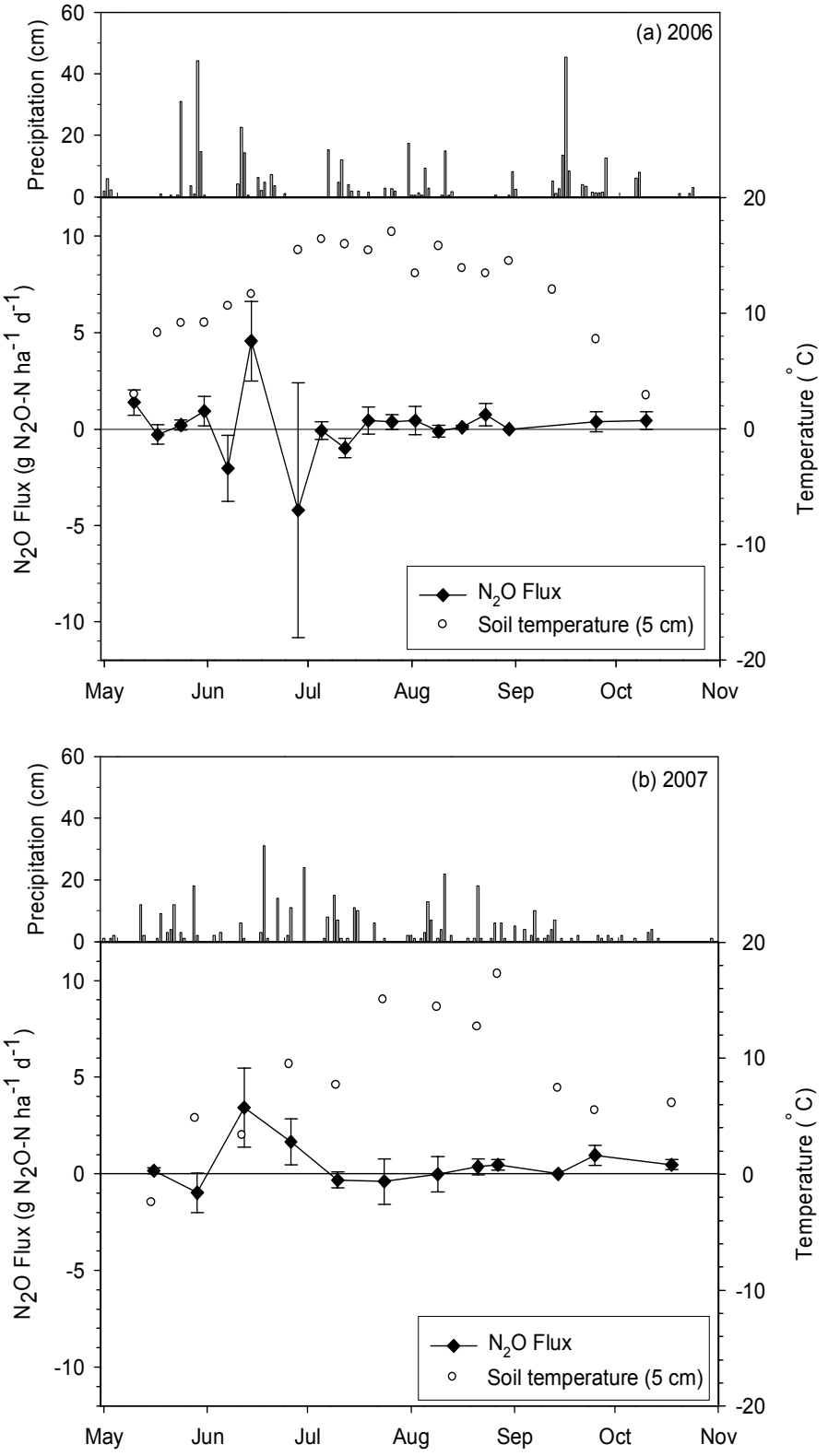


Figure 15. Old growth jack pine stand (OJP) daily nitrous oxide fluxes, precipitation (Fluxnet-Canada, 2008), and temperature (5 cm below the soil surface), from the frost-free period of 2006 (15a) and 2007 (15b). Flux values were calculated by averaging the daily flux measurements from a 20-point transect; error bars show standard error.

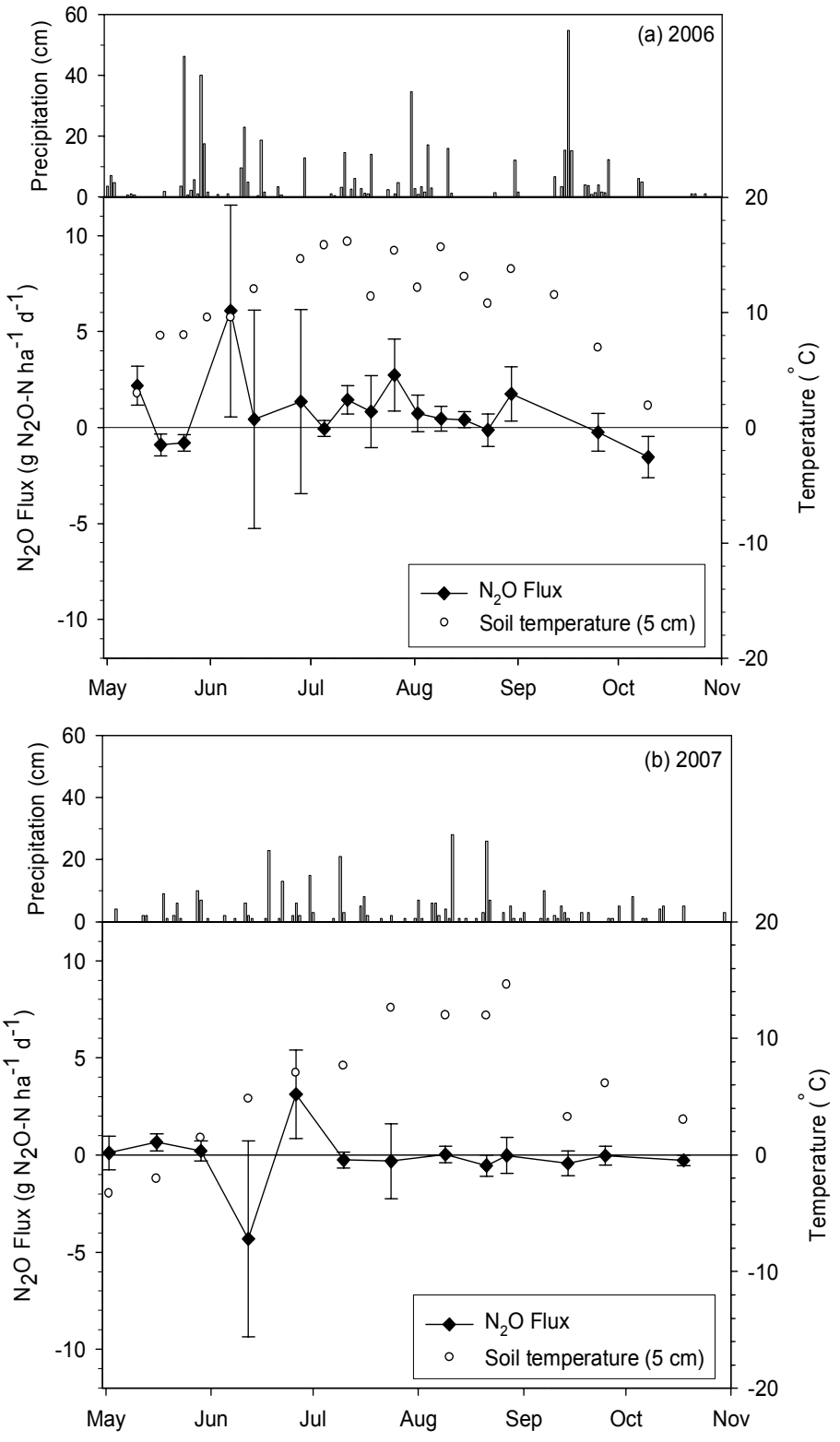


Figure 16. Old growth black spruce stand (OBS) daily nitrous oxide fluxes, precipitation (Fluxnet-Canada, 2008), and temperature (5 cm below the soil surface), from the frost-free period of 2006 (16a) and 2007 (16b). Flux values were calculated by averaging the daily flux measurements from a 20-point transect; error bars show standard error.

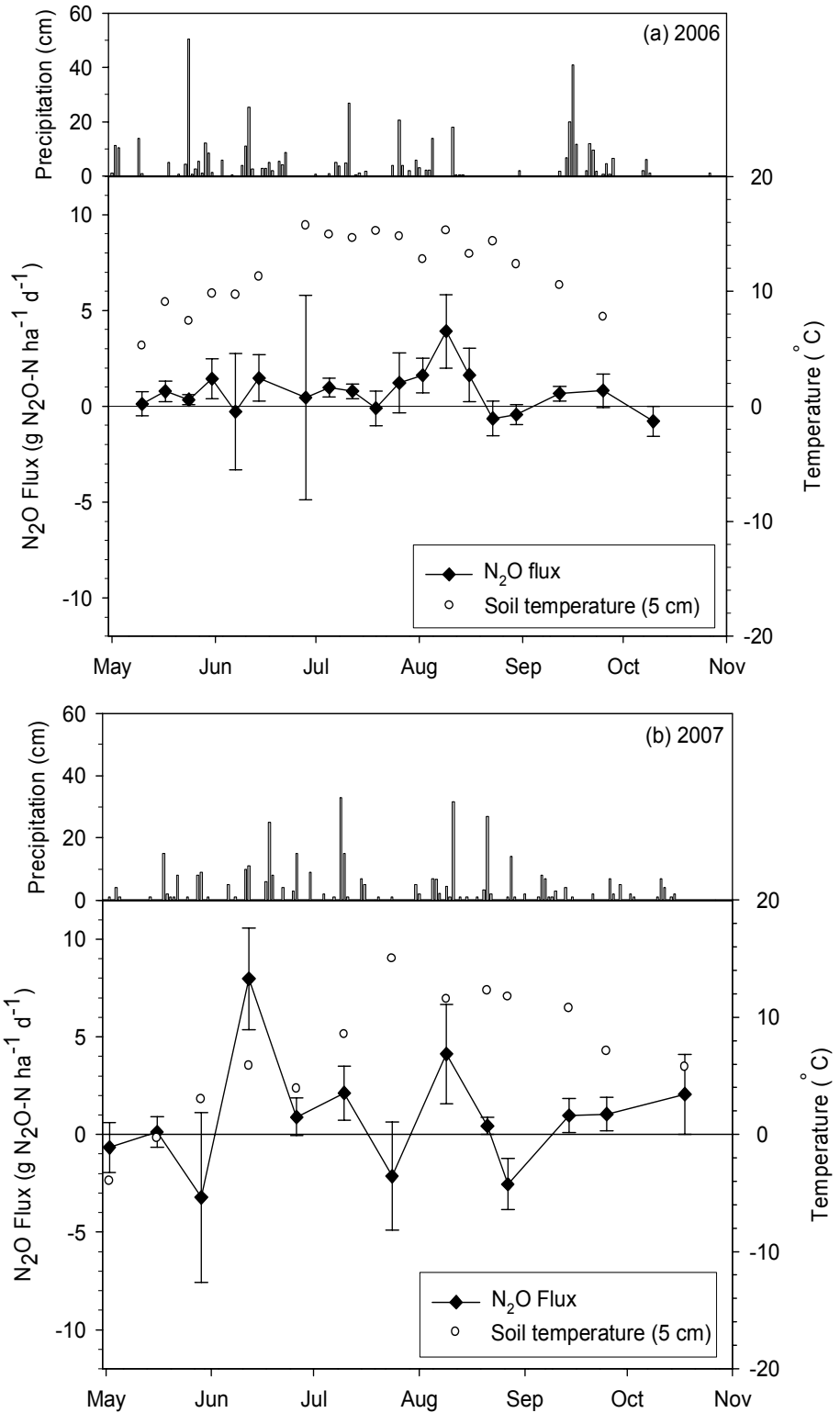


Figure 17. Old growth trembling aspen stand (OTA) daily nitrous oxide fluxes, precipitation (Fluxnet-Canada, 2008), and temperature (5 cm below the soil surface), from the frost-free period of 2006 (17a) and 2007 (17b). Flux values were calculated by averaging the daily flux measurements from a 20-point transect; error bars show standard error.

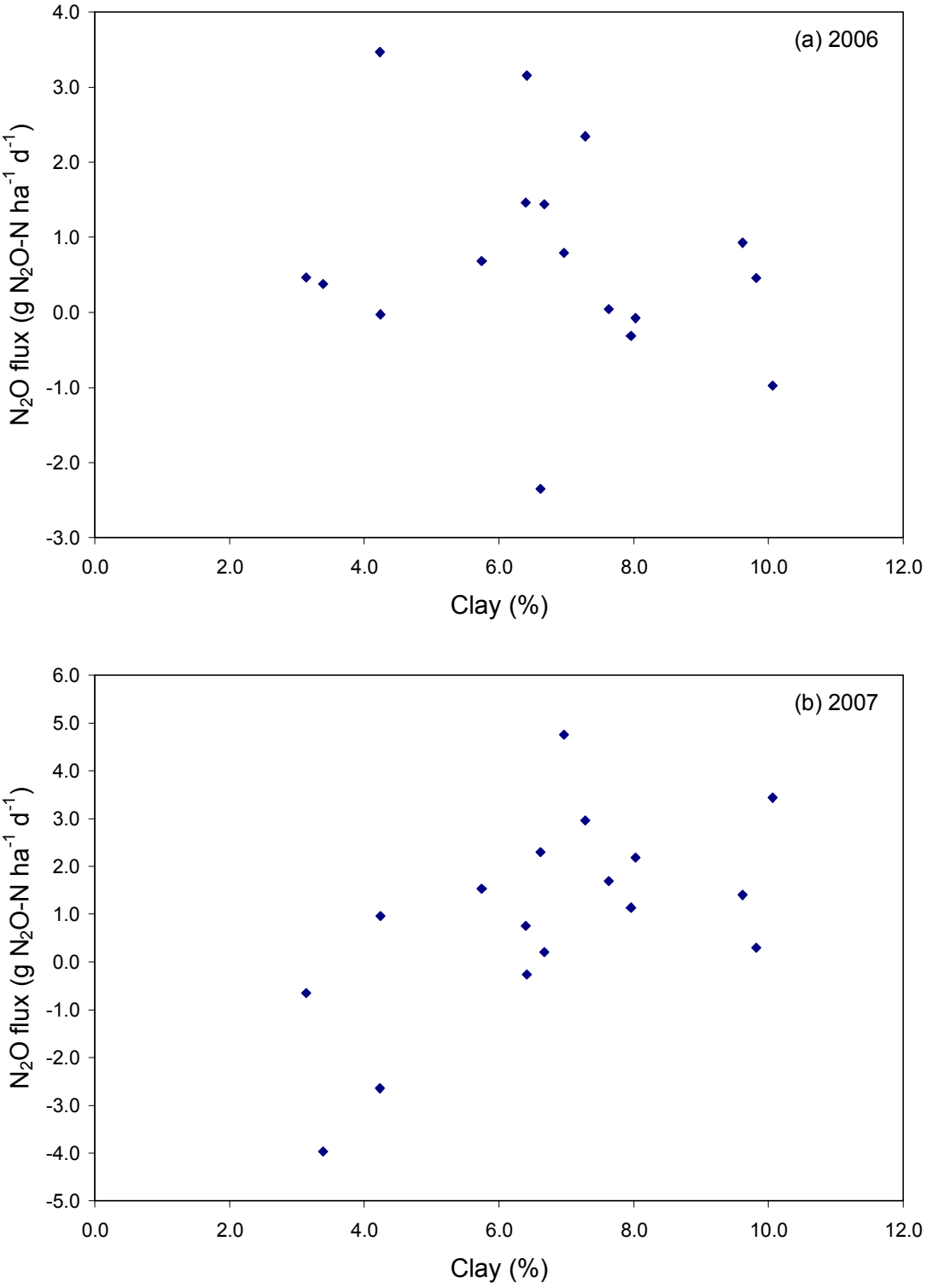


Figure 18. Old growth trembling aspen stand (OTA) average daily nitrous oxide emissions from May to October (19 dates in 2006 and 13 dates in 2007), from 17 sampling locations in (18a) 2006 and (18b) 2007, plotted against the % clay in the soil at each location. The two-tailed Pearson correlations were r = -0.24 (p = 0.36) in 2006 and r = 0.60 (p = 0.01) in 2007.

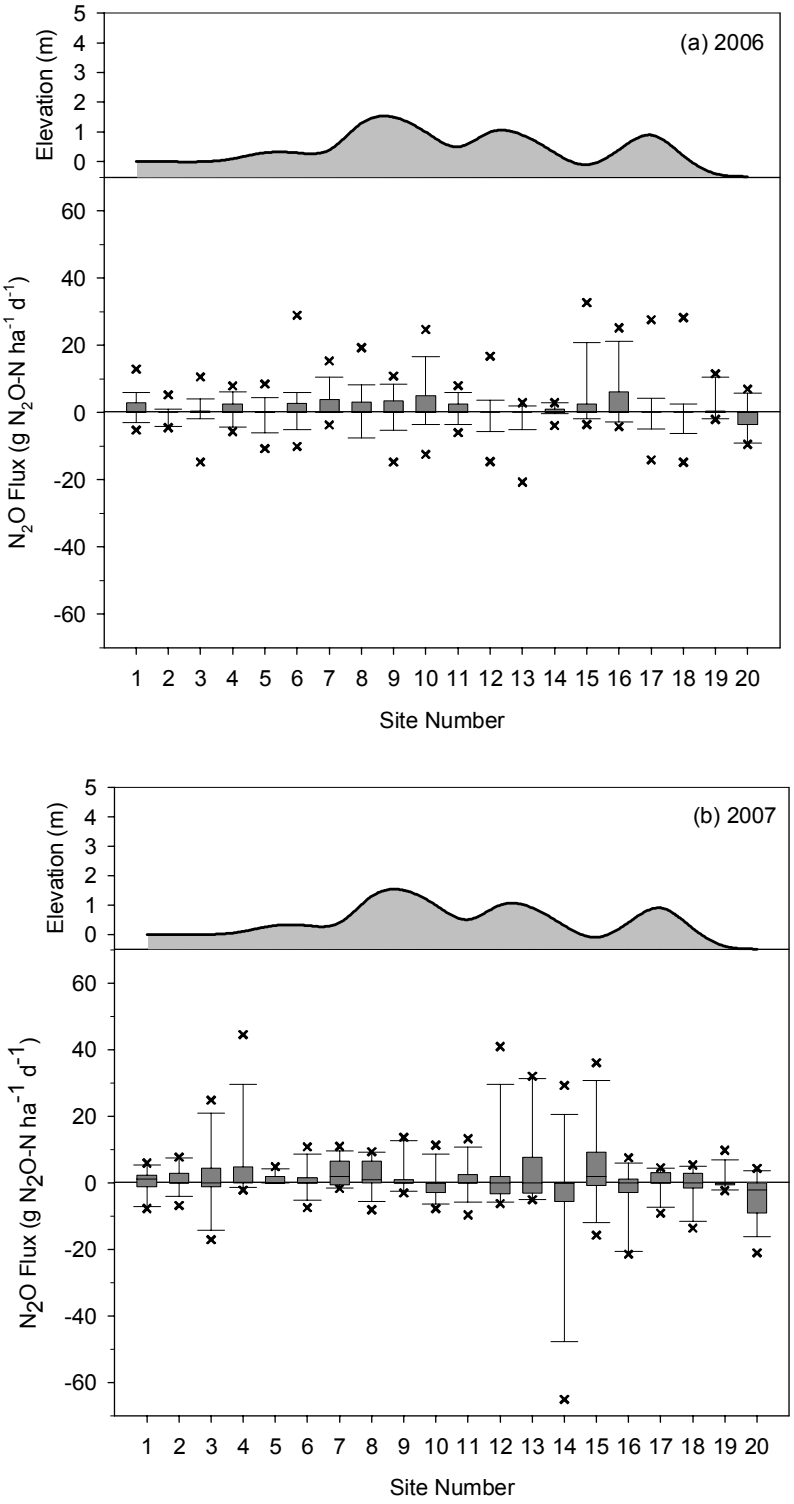


Figure 19. The range of daily nitrous oxide emissions from an old growth trembling aspen stand (OTA) measured over the frost-free period of 2006 (19a) and 2007 (19b) from each location along a transect (elevation shown by the solid black line). In 2006, emissions were measured weekly from May to August and biweekly in September and October (boxplot N=19). In 2007, emissions were measured biweekly from May to October (boxplot N=13).

3.3.3 Nitrogen cycling

The N_2O emissions from the OTA soil cores labeled with $^{15}NO_3^-$ were very low throughout both years of the ^{15}N study (Table 5). The T00 fluxes ranged from -4.24 to 1.42 g N_2O-N ha^{-1} d^{-1} and the T24 fluxes ranged from -0.03 to 0.05 g N_2O-N ha^{-1} d^{-1}. Compared to the measured chamber fluxes (Figures 15-17), these are well within the expected range of soils exhibiting background emissions. The higher T00 as compared to T24 fluxes were presumably an artifact of the sampling disturbance. As shown by the BG and labeled columns in Table 5, the added ^{15}N did not cause the flush of activity, since there were only two significant differences between the labeled and unlabeled cores throughout the course of the study, both of which were in T24 cores. Regarding the pathway responsible for the emissions, as shown by the % denitrification column in Table 5, with only one exception denitrification was responsible for <15% of total N_2O emissions. Although the results in the table are grouped into upper and lower slope cores, the difference in emissions between the slope positions was only significant once, in July 2006 ($p = 0.03$); on this date denitrification is significantly higher in the depressions than the upland positions ($p = 0.04$).

As shown in Table 6, although the inorganic N pools were small, the gross rates indicated that both pools were active. For example, in the July lower slope positions, the NO_3^- concentrations in the soil ranged from 0.00 to 0.02 mg NO_3-N kg^{-1}, while the nitrification rates ranged from 0.00 to 0.04 mg NO_3-N kg^{-1} d^{-1}. Since the production of NO_3^- was roughly twice the soil concentration, the total NO_3^- in the soil must have been consumed approximately twice every day in order to maintain the low soil NO_3^- levels; the rate of consumption was indicated by the turnover rate of 0.39 days. In contrast, the NH_4^+ concentrations on that date ranged from 0.67 to 3.34 mg NH_4^+-N kg^{-1}, while the mineralization rates ranged from 0.72 to 2.83 mg NH_4^+-N kg^{-1} d^{-1}. These ranges were more similar, with the mean production of NH_4^+ being just slightly less than the mean soil concentration. As such, the NH_4^+ remained in the soil longer, being consumed in just over a day; the lower slope turnover rate for NH_4^+ in July was 1.32 days.

Since the NH_4^+ concentration data in August were not significantly different from those in June or July, and the NO_3^- data, although significant ($p = 0.05$), was still very low (0.09 ± 0.06 mg NO_3-N kg^{-1} in upper slopes and 0.06 ± 0.09 mg NO_3-N kg^{-1} in lower slopes), the third set of ^{15}N samples was not analyzed.

Table 5. Nitrous oxide (N_2O) emissions from ten forest soil cores (five for each slope position) with (labeled) and without (background = BG) added $K^{15}NO_3^-$. Measurements for T00 were taken, on average, 20 minutes after injection; T24 measurements were taken 24 hours later. The proportion of the labeled emissions from denitrification (% Denit.) is also shown.

Year	Month	Slope Position	T00 N_2O Flux (g N_2O-N ha^{-1} d^{-1})			T24 N_2O Flux (g N_2O-N ha^{-1} d^{-1})		
			BG	Labeled	% Denit.	BG	Labeled	% Denit.
2006	June	Upper	1.22	1.42	0.03	0.00	0.01	0.65
		Lower	0.68	1.29	0.03	0.00	0.00	0.53
	July	Upper	1.32	0.98	0.72	-0.03[1a]	0.02[1b]	11.01[2a]
		Lower	0.31	1.23	1.52	-0.01[1a]	0.05[1c]	44.89[2b]
	August	Upper	-4.25	-2.35	0.03	-0.01	0.00	5.72
		Lower	-2.25	-1.83	4.48	0.01	0.01	16.17
2007	June	Upper	-1.10	-0.92	0.06	0.00	0.00	1.56
		Lower	-2.09	-0.88	0.62	0.02	0.01	4.66
	July	Upper	0.72	0.77	0.19	0.03	0.03	4.00
		Lower	0.18	0.82	0.60	0.00	0.02	2.28
	August	Upper	0.29	0.36	0.03	0.00[1d]	0.02[1e]	1.15[2c]
		Lower	0.88	0.18	0.23	0.00[1d]	0.02[1e]	3.71[2d]

[1]There are significant differences ($p = 0.05$) between BG and labeled fluxes in July 2006 ($p = 0.04$ and $p = 0.02$ for upper- and lower-slope respectively), and August 2007 ($p = 0.02$ and $p = 0.05$ for upper- and lower-slope respectively), as well as between the upper and lower slope labeled fluxes in July 2006 ($p = 0.03$).
[2]The amount of N_2O from denitrification is significantly different between the slope positions at T24 in July 2006 ($p = 0.04$) and close at T00 in August 2007 ($p = 0.09$).

Table 6. Inorganic N stocks (NO_3^- and NH_4^+), gross rates of nitrification and mineralization, and N turnover in forest soil cores taken from a boreal forest trembling aspen stand and incubated in the field for 24 hours in the summer of 2007. Missing data are indicated by ND (not determined).

Date	Slope Position	Site #	N-stocks (mg N kg^{-1} soil)		Gross rates (mg kg^{-1} d^{-1})		Turnover (d)	
			NO_3-N	NH_4-N	Nitrification	Mineralization	NO_3-N	NH_4-N
June 5	**Upper**	5	0.00	1.04	0.01	0.63	0.00	1.66
		7	0.00	0.94	0.07	2.61	0.01	0.36
		9	0.02	1.20	0.04	2.52	0.45	0.47
		13	0.00	1.48	0.02	0.48	0.00	3.08
		17	0.00	1.61	0.05	0.12	0.00	13.43
		Mean	0.00 (0.01)	1.25 (0.29)	0.04 (0.02)	1.27 (1.20)	0.09 (0.20)	3.80 (5.49)
	Lower	1	0.01	3.27	0.00	1.83	32.29	1.79
		3	0.00	2.58	0.00	ND	0.00	ND
		11	0.00	2.44	0.04	7.02	0.00	0.35
		15	0.00	8.53	0.07	ND	0.00	ND
		19	0.04	1.86	0.06	1.80	0.67	1.03
		Mean	0.01 (0.02)	3.74 (2.73)	0.03 (0.03)	3.55 (3.01)	6.59 (14.37)	1.06 (0.72)
July 19	**Upper**	5	0.00	7.84	0.00	0.50	0.00	15.79
		7	0.01	1.02	0.04	0.75	0.39	1.37
		9	0.03	1.40	0.04	ND	0.86	ND
		13	0.02	2.26	0.05	0.44	0.38	5.11
		17	0.03	0.70	0.06	0.28	0.40	2.50
		Mean	0.02 (0.01)	2.64 (2.96)	0.04 (0.02)	0.49 (0.19)	0.41 (0.31)	6.19 (6.59)
	Lower	1	0.00	3.18	0.00	ND	0.00	ND
		3	0.02	0.67	0.04	1.43	0.52	0.47
		11	0.01	1.06	0.03	2.83	0.41	0.38
		15	0.01	3.34	0.02	1.12	0.62	2.97
		19	0.02	1.05	0.04	0.72	0.40	1.45
		Mean	0.01 (0.01)	1.86 (1.29)	0.03 (0.02)	1.52 (0.91)	0.39 (0.24)	1.32 (1.21)

3.4 Discussion

3.4.1 Methane emissions

Each of the sites had a unique pattern of CH_4 flux. The OJP site was a slight sink, the OBS site oscillated above and below zero but was cumulatively negligible, and the OTA site was a substantial source.

The OJP soils oxidized CH_4, consistently acting as a slight sink over the two years of the study (Figure 4). This result was consistent with Whalen et al. (1992), as shown in Table 1; they also studied CH_4 emissions from Brunisolic soils and found them to be a slight sink. The fact that OJP acted as a sink likely reflected the sandy soil at the site, which was well-drained and therefore unsuited to the development of an anaerobic methanogen community. Coarse-textured soils have been documented as supporting CH_4 oxidation by enhancing gas diffusion (CH_4 and O_2) into the soil (Saari et al., 1997). Diffusion would be inhibited by water in the soil, though, explaining why oxidation in 2006 decreased as WFPS increased (Figure 7). In addition, the flux values at this site were inversely correlated with SOC, meaning that consumption increased (fluxes became more negative) at sampling points with more SOC (Figure 10). This relationship was possibly due to soils with more SOC having higher microbial activity and thus being more capable of supporting an aerobic methanotroph community. Bender and Conrad (1994) demonstrated that within well-aerated soils, areas of high CH_4 oxidation were those with localized higher surface area and nutrient concentration, both of which would be directly related to SOC (Sparks, 2003).

The lack of emissions from OBS (Figure 5) was surprising, considering that peatlands are the single most important CH_4 source globally and that northern peatlands are thought to contribute 34-60% of global wetland emissions (Vasander and Kettunen, 2006). It was also surprising in light of the literature reviewed in Table 1, where the only Organic soils that did not emit CH_4 were those in an ombrotrophic bog (Moore and Knowles, 1990) and a raised bog (Waddington and Roulet, 2000). The site conditions at OBS seemed ideal for CH_4 production; the water table was at or close to the surface for most of the year, and the soil had an accumulation of organic matter in the peat layer, providing both anaerobic conditions and ample substrate for methanogenesis (Section

2.1). It is possible that emissions were not occurring because there were more thermodynamically-favorable electron acceptors present. Technically, the reduction sequence in anaerobic soils dictates the use of nitrate, ferric iron and sulfate before carbon dioxide (Chidthaisong and Conrad, 2000). Judging from the amount of nitrate seen at the trembling aspen site (Table 6), it seems unlikely that there would have been significant amounts in the fen. However, ferric iron was not measured, and SO_4 may have also been playing a role. The levels of SO_4 measured in the water at OBS (Table 3) seemed too low to completely account for the lack of emissions, but it was notable that when compared to several other wetlands within that ecodistrict that were sampled and assessed for water chemistry in July 2007 (Tables A.1 and A.2), the OBS concentrations were, on average, an order of magnitude higher than any of the others.

The lack of emissions at OBS may also have been a balance between production and consumption. Although the anoxic conditions of the soil precluded aerobic methane oxidation there may have been some anaerobic oxidation of methane (AOM). Smemo and Yavitt (2007) confirmed the occurrence of AOM in several northern peatlands, although they were unable to explain the exact mechanism. They found that the process was more important in wetlands that were not isolated from the water table, hypothesizing that whatever the electron acceptor was, it was being supplied via the groundwater. This would correspond well with OBS, as it is not isolated from the water table. In marine systems, the electron acceptor for AOM is sulfate (Hoehler et al., 1994), which, as mentioned above, was present at the site. Another choice for an electron acceptor in anaerobic environments is dissolved organic matter (DOM). Heitmann et al. (2007) demonstrated that in peat soils, DOM was quite likely contributing to heterotrophic respiration in one of two ways: the quinone groups in the DOM were acting as electron acceptors, or the DOM was oxidizing H_2S to thiosulfate, which could then act as an electron acceptor and be reduced back to H_2S. As the OBS site did have an accumulation of peat, there was likely ample DOM in the soil to act as electron acceptors for CH_4 oxidation. In addition, SOM was inversely correlated with CH_4 emissions at OBS in 2006 (Figure 11), indicating that OM could be enhancing CH_4 oxidation. To further this point, it is possible that the age of the organic matter in the peat may have played a role in the lack of CH_4 emissions. As the organic matter in the

peat was likely quite old, with all of the easily decomposable material gone, it may have been able to function as an electron acceptor far more readily than being decomposed to form CH_4 (Moore and Basiliko, 2006). In 2007, the CH_4 emissions were negatively correlated with the clay content of the soil (Figure 13). Although areas with clay would clearly have more OM than those without (Sparks, 2003), the relationship with clay may have also been an indication that other electron acceptors, such as exchangeable Fe and Mn (Smemo and Yavitt, 2007), were an important component of oxidation in 2007.

The CH_4 emissions from the trembling aspen site were by far the most dramatic (Figure 6), with values comparable to the Organic soils listed in Table 1. The OTA emissions were controlled by a combination of temperature, moisture and OC. Although significantly related to temperature in both years (Figure 8), the OTA emissions could not be explained by temperature alone; in 2006, high emissions did not occur until soil temperatures reached 12°C, yet in 2007 they began as soon as temperatures were past 4°C. An additional controlling factor was clearly the presence of water, as flooded and/or moist soils were the only areas which ever exhibited high emissions (Figure 14). The presence of water as a control may partially explain the variation in temperature response between the two years. If the years preceding this study did not have surface ponding, as discussed in section 3.3.1, this suggests that the population of methanogens may have been very small during 2006 (Basiliko et al., 2003), so that high emissions could not occur until later in the season once the soils had warmed up and the methanogen population had adjusted to the more favorable soil conditions (Mayer and Conrad, 1990). Emissions were then cut off when the ponds dried up in August. The next summer the more abundant community was already in place, so that as soon as the temperature was above 4ºC, emissions began to occur; these once again continued until the ponds dried up. In 2007, a major precipitation event coupled with an unseasonably warm fall, allowed emissions to re-start and continue until, we presume, the dropping temperatures again cut them off.

As noted in Section 3.3.1, the CH_4 emissions at OTA may have been biased by the time of day that they were sampled. Figure 9 showed that CH_4 exhibited a diurnal flux, and that by sampling in the early afternoon we were likely capturing emissions when they were at or near their peak. Phipps (2006) measured CH_4 emissions from

wetlands in the prairie region of Saskatchewan and also noted a diurnal flux. In order to account for it, she measured CH_4 flux over a full 24 hour period, three times over the growing season, in order to calculate a correction factor that could be used when scaling up emissions measured in the daytime. Using her correction factor, the cumulative emissions for the trembling aspen site would decrease from 46.7- to 35.0- kg N_2O-N ha^{-1} d^{-1} in 2006 and 196.0- to 146.6- kg N_2O-N ha^{-1} d^{-1} in 2007.

Other studies have reported high emissions from flooded forest soils, although not in undisturbed forests. Jugnia et al. (2005) and Matthews et al. (2005) studied the effect of artificially flooding boreal forest soils to create reservoirs. Both studies found that the flooded soils not only emitted CH_4, but that the magnitude of the emissions was higher than those from non-flooded peat or soil, and permanently flooded lake sediment. The magnitude of the fluxes may be in part due to the episodic nature of the flooding in these wetlands, which mimic the natural process that we observed at OTA. During non-flooded years, there is likely a build-up of organic matter in the soil, which then provides abundant substrate for the methanogens once the soil is flooded. As shown in Figure 12, emissions at the site were correlated with OM in 2006, but the significant relationship was clearly due to the two very high points, both of which were from depressions. If the depressions had deposits of fresh organic matter inputs, there would be an abundance of labile materials that could be easily decomposed by methanogens (Moore and Basiliko, 2006). This hypothesis could also explain the lack of emissions seen in the depression at #11; if it experienced some degree of flooding each spring, the depression would not get periodic inputs of fresh organic matter from shrubby vegetation. It may be that the labile OC in this wetland is gone and is not being replaced every few years, making it a less suitable environment for methanogens than the other depressions.

3.4.2 Nitrous oxide emissions from OJP and OBS

Although the two sites were quite different from one another, both OJP and OBS had very low N_2O emissions over the course of the two years (Figures 15 and 16), and were well within the ranges noted in Table 1. At OJP, the coarse-textured soil would have prohibited anaerobic conditions from occurring for any length of time after a

rainfall event, thus minimizing the likelihood of N_2O emissions from denitrification or nitrifier denitrification. In addition, the very poor nutrient status of the soil would result in a lack of both C as a growth substrate for the denitrifying community, and excess inorganic N that could be used as a terminal electron acceptor (Borken and Beese, 2005). At the black spruce site, however, the water table was close to the surface for most of the summer, and there was an abundance of organic carbon present. One explanation could be that the lack of N_2O at this site indicated that nitrogen was being completely reduced to N_2, rather than stopping at N_2O. Startsev and Lieffers (2007) studied the effect of drying and wetting on feathermoss from a boreal site in Alberta. They found that the moss was not resistant to changes in moisture, and that each time it was re-wetted, a flush of N gases were emitted, the majority of which were N_2. They suggested that rather than contributing to the nutrient status of the soil, the mosses were intercepting N from precipitation and litterfall, storing it in tissue and then emitting it as they experienced dry and wet cycles. If this was the case at OBS, it would explain why there was not enough inorganic N reaching the anaerobic soils to generate significant N_2O. To further this explanation, research has indicated that the inorganic N cycle may be unimportant for plant nutrition in boreal systems, as many plants have been proven to be capable of using simple organic N sources directly (Persson et al., 2003; Nordin et al., 2001). Therefore, the lack of inorganic N in the rooting zone for plants besides mosses would not be an issue, as they could access their N from the amino acid N pool.

3.4.3 Nitrogen cycling and N_2O emissions from OTA

At OTA, the N_2O fluxes from the *in situ* chamber measurements (Figure 17) and ^{15}N incubations (Table 5) were low in both years of the study. In 2007, the chamber measurements were found to be correlated with the amount of clay in the soil (Figure 18). Although a positive correlation with clay could have indicated that N_2O emissions were from denitrification and therefore higher in areas with more moisture (clay being an indication of water-holding capacity), emissions at OTA were not significantly different between the flooded depressional areas and the uplands (Figure 19). In addition, the $^{15}N_2O$ data indicated that very little of the emissions were a result of denitrification (Table 5), but instead a nitrification-related process such as nitrification,

chemodenitrification or nitrifier-denitrification (Section 2.2). Bedard-Haughn et al. (2006) observed a similar situation in the grassland region of Saskatchewan, where ^{15}N-labeled emissions had been identified as being nitrification-related, but were also correlated with WFPS; these emissions were suggested as being the result of nitrifier-denitrification since the pathway requires short-term anaerobic conditions or anaerobic microsites (both related to WFPS) to occur. This explanation would also hold true at OTA. Sampling points with high clay in the soil would be more likely to have both aerobic and anaerobic microsites; this would create regions of low oxygen availability where both nitrification and N_2O production could occur via nitrifier denitrification.

The emissions from both $^{15}NO_3^-$-labeled (Table 5) and $^{15}NH_4^+$-labeled (not shown) soil cores were well within the range of those from the unlabeled background cores. In fact, although the numbers were not reported, the N_2O flux from the cores with added NH_4^+ were even lower than those from the NO_3^- cores, despite a nitrification-related process being the dominant pathway for N_2O production. This could indicate a flaw in the labeling, in that NH_4^+ was not being evenly distributed. However, the lack of additional N_2O from the added N could also suggest that the soil processes were not N-limited, or possibly part of a tightly-coupled system, in which the products of each N process were immediately consumed as substrate for the next stage of the N cycle. If nitrifiers were adapted to using NH_4^+ as it is mineralized, rather than accessing the exchangeable NH_4^+ pool, it would explain why there was a negligible response to the added $^{15}NH_4^+$.

The rates of mineralization and nitrification measured at OTA (Table 6) were within the low range of other reported values (Table 2) and consistent with the finding by Booth et al. (2005) that soil pools of NO_3^- and NH_4^+ from many ecosystems tend to turn over daily. In terms of being a control on N_2O emissions, the gross cycling rates showed that in addition to the NO_3^- pool being very small at any one time and turning over rapidly, the total amount of NO_3^- cycling through the soil was minimal. So, although nitrification was occurring, and through a nitrification-related process resulting in some N_2O emissions, those emissions were very low. The gross rates also furthered the idea that boreal plants may be accessing a significant amount of organic, rather than simply inorganic, N sources. The very low concentration of NO_3^- and NH_4^+ present in

the soil at any point in time coupled with the daily turnover rate indicated that while the system was tightly-coupled and therefore highly conservative, the little inorganic N that was present was unlikely to be an adequate volume to sustain tree growth. Therefore, it is likely that the plants are accessing the majority of their N requirement from an organic form.

3.5 Conclusions

According to this study, soils in mature stands of jack pine and black spruce in Saskatchewan's boreal forest should not be large contributors of CH_4. In fact, jack pine soils should be a slight sink every year. Trembling aspen soils would be a significant source, though, in years when significant flooding of upland depressions occurred. Precipitation data from Prince Albert, Saskatchewan (Environment Canada, 2008), shows that between 1947 and 2007, there were four years (not including the years of this study) that had atypically high precipitation. So, in the last 60 years, there was likely six years when ponding was present in upland forest soils. Emissions of N_2O should not occur from soils in any of the three stands from this study. The results of the gross N cycling at the trembling aspen site suggested that the low N_2O emissions were due to a conservative, tightly-coupled system that precluded any significant amount of inorganic N from cycling through the soil, preventing the production of gaseous N. Further studies should validate the observations for both CH_4 and N_2O in other similar ecosystems, as the stands in this study were not replicated.

In recent decades, there has been concern that anthropogenic practices such as harvesting and fire suppression are responsible for observed decreases in the biodiversity of forest plant and animal communities (Nitschke, 2005). There is also the possibility that disturbances such as acid rain and nitrogen deposition, which are currently minimal in Saskatchewan, could increase. Finally, there is the future threat of climate change and how it could further alter forest ecosystems. The measurements from this and similar studies may be useful as threshold values for estimating the impact of disturbances, or the success of reclamation in altered forest areas, on forest CH_4 and N_2O emissions. Naturally, they will also be useful as a marker to indicate how greenhouse gas emissions change over time.

4. CONTEXT AND SIGNIFICANCE

4.1 Boreal soils in the Canadian context

4.1.1 Methane and nitrous oxide flux

According to the Environment Canada National Inventory Report for 1990 to 2005 (Environment Canada, 2007), Canada's total greenhouse gas emissions in 2005 were 747, 000 kt CO_2 equivalents. This included 5200 kt CH_4 (15% of total emissions) and 140 kt N_2O (6% of total emissions). The large majority of the emissions (81.5%) came from the energy sector, with agriculture (7.6%), industrial processes (7.1%) and waste (3.7%) making up the remainder. It is notable, however, that fluxes from managed forest lands - including wetlands - were not included in these totals. Saskatchewan was responsible for 9.6% of Canada's national emissions, making it the country's fourth greatest contributor after Alberta, Ontario and Quebec; emissions in the province increased approximately 1.5 times from 1990 to 2005.

In the 2005 National Inventory (Environment Canada, 2007), there were three categories of soil-related emissions that reported values for CH_4 and N_2O: agricultural soils, managed forests, and managed wetlands. Agricultural soils were not reported as having CH_4 fluxes, but emitted 76 kt of N_2O, 22% of which came from Saskatchewan. The estimates of emissions from managed forestry regions were 240 kt CH_4 and 10 kt N_2O for forest land, and 2 kt of CH_4 and 0.06 kt N_2O for wetlands; these were not divided into provincial emissions, as they were not officially included in the reported totals. In comparison, assuming the land area of Saskatchewan is 651,036 km^2 (Natural Resources Canada, 2001), that emissions in all managed forests in Saskatchewan are similar to those reported in this study, and that the land areas associated with each stand type as outlined in Section 2.5 are accurate, Saskatchewan's potential emission totals from the boreal forest would be: -3.8 kt CH_4 and 0.27 kt N_2O from jack pine stands, 0.47 kt CH_4 and 0.21 kt N_2O from black spruce stands, and 779 kt CH_4 and 0.99 kt N_2O from trembling aspen stands.

4.1.2 CH_4 emissions

Although the number was a rough estimate, the scaled up CH_4 emissions from the trembling aspen site in this study (Section 4.1.1) resulted in Saskatchewan forest emissions that were three times higher than the reported emissions from managed forest lands in all of Canada. It is clear, then, that emissions from managed forests need to be included in national greenhouse gas estimates, and these estimates must be able to model and account for CH_4 emissions from episodically flooded wetlands.

According to Fluxnet-Canada (2007), in the years leading up to this study, precipitation at the trembling aspen site went through significant changes. From 2001-2003, cumulative precipitation at the site totaled 230 mm, 280 mm and 260 mm; compared to the average accumulation of 467 mm, these were clearly drought years. In 2004 and 2005, precipitation rose to 660 mm and 620 mm respectively. However, at the beginning of this study (2006) there was still abundant vegetation in many of the depressional areas that was not killed by water stress until the following year. So, it is likely that the precipitation from 2004 and 2005 recharged the water table, but did not result in significant standing water until 2006, when the cumulative precipitation was 620 mm. In the second year of the study, 2007, the cumulative precipitation was 550 mm, slightly less than the previous years, but this was the year that exhibited the most significant CH_4 flux. As discussed earlier, the increase in CH_4 from 2006 to 2007 was likely due to a growing community of methanogens and the presence of labile OC.

In order to model CH_4 emissions from this landscape, then, several factors would need to be addressed. To identify possible areas of emissions one would need to assess topography, including catchment area and spillover depth for each depression, and soil texture, which would affect the water-holding capacity of the soil. Predicting years with high emissions would require understanding of the water table depth as affected by previous years of precipitation, and temperature, which would control the rate of pond dry-down in flooded areas. The strength of emissions would be dependent not only on flooded conditions, but also the amount and type of organic matter inputs in the years leading up to flooding, and the number of years that flooded conditions had occurred, as both of these would affect the size of the microbial community. Finally, the spatial extent of soils emitting at any one time would be dependent on the amount of

flooding in that year. In this study, the sampling point closest to the center of the pond (#20) did not emit CH_4 until later in the season than the other points, when it had dried down past a certain threshold (although not determined in 2006, the threshold depth in 2007 was 30 cm). This threshold would need to be understood in order to correctly model emissions changes over the season.

4.1.3 Nitrogen cycling

Measurements of N cycling in the boreal forest indicate that mineralization and nitrification do not account for the N uptake of many forest stands. Research has suggested that the bulk of the N demand in the boreal forest may be supplied by organic N. Although it is not a significant source of N for most types of vegetation, many boreal forest plants have been found to be capable of using organic N as a nutrient source (Kielland, 1994; Näsholm et al., 1998). It has been suggested that this is because the organic N pathway is an adaptation by plants in ecosystems that are strongly N-limited, such as arctic, alpine and boreal regions (Harrison et al., 2007).

Boreal forest research regarding organic N provides a wide range of information supporting its significance to plant nutrition. Persson and Näsholm (2001) did an extensive lab study with 31 common boreal forest species and found that all of them could take up amino acids from the incubation solution, regardless of whether or not they were aided by symbiotic relationships such as mycorrhizal fungi. This almost universal ability of plants to use DON has been noted in many studies (Kielland, 1994; Nordin et al., 2001; Harrison et al., 2008), and only some reported that the relative ability to do so differed between species. It is suggested, then, that the predominance of the DON uptake pathway in the boreal forest is not so much related to differences in plant physiology, but is instead a reflection of the fact that soils in the boreal ecosystem often have an amino acid pool up to four times that of NH_4^+ and NO_3^- combined (Kielland et al., 2006). This idea is supported by many studies, which have shown that although plants still prefer inorganic forms of N, their relative uptake of DON and DIN (dissolved inorganic N) is directly proportional to the availability of each N pool (Nordin et al., 2001, 2004; Kielland et al., 2006). Further support of this idea comes from studies of amino acid turnover in the boreal forest, which have found that turnover

rates are very rapid, and can be up to 20 times per day (Jones and Kielland, 2002). Kielland et al. (2007) determined that the rapid turnover they observed in a boreal forest soil could potentially provide more than enough N to supply the vegetation demand, without any contribution from the inorganic N pools. This was further corroborated by Kranabetter et al. (2007) who found that DON was significantly related to boreal plant uptake. The group went on to show that when comparing N supply with stand height, the combined DIN and DON pools were linearly correlated, whereas DIN by itself was not. Despite the strength of all of these arguments, there is still considerable controversy regarding whether or not these studies were reliable. The problem is methodological, related to the use of isotopes to trace the organic N.

Isotope studies of DON uptake have several weaknesses. Isotopes can be used in lab studies with no other N sources (Persson and Näsholm, 2001) or no active microbial biomass (Taylor et al., 2004) very successfully, but in field situations they are less dependable. Since amino acid N is mineralized by microorganisms in the soil, tracing labeled amino acids from the soil into a plant does not guarantee that the amino acid has been taken up intact (Jones et al., 2005). Most DON uptake studies use doubly labeled carbon (C) and N in the amino acids (^{13}C and ^{15}N), and maintain that if the ratio of ^{13}C:^{15}N recovered in the plant is significantly related to that of the initial amino acid, this suggests that the amino acid was indeed directly accessed by the plant (Schimel and Chapin, 1996). While this is strong evidence, there are a number of uncertainties associated with it. Many studies find that instead of being incorporated into the plant, ^{13}C is recovered as CO_2 gas; since both the soil microorganisms and roots can respire CO_2, there is no way to know where the $^{13}CO_2$ originated (Persson et al, 2003). In some cases, the labeled ^{13}C is either diluted too much from the amount of C found in the plant or is added in such small amounts that it cannot be distinguished from background levels of ^{13}C (Näsholm and Persson, 2001). In cases where both labels are recovered in the plant, one cannot be certain that they were not mineralized in the rhizosphere and taken up separately, rather than as an intact amino acid (Jones et al., 2005).

Although techniques have not been perfected to study DON uptake, it is still vital that research continues to be done in this field. If plant use of DON is a significant source of plant nutrition in boreal systems, then it explains the lack of reported N_2O

emissions from undisturbed forests, and suggests that they will always be negligible from undisturbed soils, as there is no known mechanism for N_2O to be emitted if N does not cycle through the inorganic pools (Section 2.2).

4.1.4 Gas fluxes from frozen soils

Although not included in this study, CH_4 and N_2O fluxes have been observed from soils during the winter months and especially during spring thaw. Frozen soils tend to be a slight sink of CH_4 (Rodionow et al., 2006), but a source of N_2O (Teepe and Ludwig, 2004; Ludwig et al, 2006). The N_2O has been identified as being predominantly denitrification-related, but significantly related to nitrification rates, as this pathway provides the substrate for N_2O production (Oquist et al., 2007).

According to Oquist et al. (2004), N_2O emissions occur in anoxic microsites within the soil that have not yet frozen; this gas is then emitted when soil thaws. They observed that up to 20% of soil water could be unfrozen at -5ºC, and this water became enriched in nutrients due to cell lysis and exclusion from ice formation, as the temperature dropped. The increase in nutrients in turn caused an increase in the rate of N_2O emissions as the temperature decreased from 0 ºC to -4 ºC. Part of that N_2O increase may have also been due to the inhibition of N_2O reductase at low temperatures; as temperature drops and N_2O can no longer be reduced, the former emissions of N_2 begin to be emitted as N_2O. However, Oquist et al. (2004) also postulated, based on their results, that mineralization ceased at -9ºC, removing the source of inorganic N for denitrification.

Although it has been noted that winter and spring thaw emissions of N_2O can result in 50% of cumulative annual N_2O from a soil, these are generally in soils that do not have very poor nutrient status (Rodionow et al., 2006). Nevertheless, even if one assumed that this study missed 50% of N_2O emissions, doubling the values in Table 4 would not increase emissions to a significant level as compared with the agricultural soils discussed in section 4.1.1. In addition, the temperatures in the boreal regions of Saskatchewan drop below -9ºC very quickly in the winter (Fluxnet-Canada, 2008). Unlike more temperate regions, where N_2O production in microsites may continue

through most of the season, mineralization would be cut off very quickly in boreal forest soils of Saskatchewan.

4.2 Disturbances

Based on the results of this study and the literature review of similar studies, CH_4 and N_2O emissions from undisturbed boreal forest regions would not be expected to be significant in most years. In fact, the only major source of CH_4 should be in episodically flooded depressional areas with fresh organic matter inputs. If the hypothesis that the majority of N-cycling is through organic forms, there should never be a case of high N_2O. Therefore, the next step would be to ascertain what occurs in disturbed regions, where these patterns of emissions may be changed through outside influences.

The Canadian boreal forest experiences several different types of disturbance, both natural and man-made. Although Saskatchewan's forests experience a variety of these, the three disturbances that are currently the most widespread are: fire, harvesting and cultivation. The way in which these disturbances affect soil processes often depends not only on their severity, but also how frequently they reoccur. Chronic disturbances such as harvesting and cultivation cause very different changes in the soil environment than do single - albeit severe - disturbances like fire (Vitousek et al., 1989).

4.2.1 Fire

Historically, fire intervals in the boreal forest were around 30 to 40 years (Larsen, 1996), but they currently range from 75 to 150 years (Gutsell and Johnson, 2005). Fires began to be suppressed in the early 1800s when wide-scale development of North America commenced. After several catastrophic fires resulting from a build-up of flammable material, policies were changed in the 1930s to include some prescribed burns, but these are still uncommon in many areas due to the risk associated with them (Busenberg, 2004).

Although there have been few studies looking at greenhouse gas emissions after fire, the potential effects can be postulated by examining how fire changes the soil

environment. There are three general effects of fire on soils: heating of soils and plants, removal of litter and standing crop, and redistribution of nutrients (Raison, 1979). Each of these has implications for changing how C and N cycle, and thereby affecting the emissions of CH_4 and N_2O. The magnitude of these effects is in turn dependent on the intensity and severity (spatial extent) of the fire.

Low temperature fires may function simply to release nutrients to surviving plants and microorganisms, and have little impact on the soil environment. However, as temperatures increase, the effect on the soil environment also increases. Depending on the severity of the fire, forest soil bacterial communities can be decreased by up to 74% (Smith et al., 2008). For example, although mineralizing bacteria can survive upwards of 100ºC, nitrifiers are killed once temperatures exceed 53-58ºC. So, although accumulations of NH_4^+ are often noted after fires, there is rarely an accumulation of NO_3^- (Raison, 1979). From a greenhouse gas perspective this is a good thing; since nitrifiers and denitrifiers are responsible for N_2O emissions, one would not expect to see increases in N_2O following a moderate to severe fire. However, the continued lack of N_2O would be dependent on how quickly vegetation re-established at the site in comparison with the microbial community. In areas of CH_4 emission it is possible to see continued fluxes after a fire, since some methanogens have been identified as surviving temperatures up to 110 ºC (Huber et al., 1989).

Burning of litter and standing biomass causes the most significant flux of nutrients from the system through volatilization. On average, a stand will require 10 years to recover its initial concentrations of C and N after a fire (Johnson and Curtis, 2001). In boreal peatlands, burning of litter can cause far-reaching effects beyond the immediate losses. Loss of primary productivity, increased soil temperature, respiration and decomposition, increased nutrient availability and water table fluctuations all provide ideal conditions for CH_4 production (Zoltai et al., 1998). Boreal wetlands have been documented as doubling their CH_4 emissions after a fire (Levine et al., 1990). In addition, Hogg et al. (1992) studied secondary losses of ash and charcoal, and found that inputs of these materials to adjacent, unburned areas could increase their CH_4 emissions by up to 8 times.

Removal of standing biomass also changes the soil micro-environment, as the soil becomes more exposed to sunlight once the forest canopy is removed. The extent of removal will determine how much the plant community shifts after a fire. If the fire was only moderately severe, so that there is enough shade remaining for the immediate re-emergence of shade-tolerant species, the stand will recover much more quickly. If increased sunlight allows invasive species to move in, it will take many more years before a late successional stand re-establishes at the site (Kemball et al., 2005). Stand recovery is also strongly dependent on the original stand composition. Jack pine trees are adapted to fire and have serotinous cones that release the great majority of their seeds only when heated; these stands will return much faster after a fire than stands that are dependent solely on the original seedbed (Beland et al., 2003). The recovery rate of a stand is significant in terms of greenhouse gas emissions. Literature reports that N cycling increases in early-successional forests recovering from disturbance (Vitousek et al., 1989), which increases the likelihood of N_2O emissions. The speed with which vegetation re-colonizes would also affect the moisture of the soil, as it is partially controlled by transpiration (Sullivan et al., 2008). Open sites with very little vegetation are more likely to have anoxic regions which can lead to both denitrification and methanogenesis (Sections 2.1 and 2.2).

Redistribution of nutrients from a fire occurs not only through volatilization, but also leaching and erosion. Ash inputs from fires can cause soils to become hydrophobic, decreasing the opportunity for anaerobic gas emissions, but increasing nutrient loss through run-off (Raison, 1979). However, despite the added potential for nutrient loss, soils often recover or enhance their initial nutrient concentration provided that plants succeed promptly (Certini, 2005). One reason for this immediate turnover is the addition of charcoal by fire, which can provide many benefits to the soil. Zackrisson et al. (1996) reported that the presence of charcoal enhances microbial biomass in humus, improves decomposition of plant litter, catalyzes ecological soil processes in early successional boreal forests, and ultimately plays an important role in the long-term productivity and functioning of the ecosystem for approximately 100 years. Deluca et al. (2006) went on to look specifically at charcoal with regards to N cycling and found that the presence of charcoal in an area of excess NH_4^+ (as is common after fire)

enhances net and gross nitrification. This could mean that after nitrifiers recover from a fire, N_2O emissions are elevated until the system recovers its original conservative nature.

4.2.2 Harvesting

Overall, 59% of the forests in Canada are considered suitable for producing marketable timber and less than 7% of the most productive ecozones are protected from harvest (Environment Canada, 2003). Therefore, it is vital to understand how harvesting may change soil processes that lead to greenhouse gas emissions.

Similar to fire, harvesting removes standing biomass and affects the soil microenvironment. Westbrook et al. (2006) studied two harvested boreal forest stands in Ontario and noted that, on average, clear-cutting increased soil temperatures by 2- to 3-°C. Although they didn't note any changes in the upland stand, increased temperatures in the peatland increased mineralization 50-fold and nitrification 9-fold. This has significant implications for increased N_2O production. Increases in temperature have not been noted to affect CH_4 flux in upland sites, as these are generally areas of CH_4 oxidation, which is most affected by diffusion of CH_4 and O_2 into the soil (Sullivan et al., 2008). However, in peatland or upland depressions with ample substrate, increased temperatures could significantly increase CH_4 production (Vasander and Kettunen, 2006). The harvest method will also have some control on the overall harvesting effect. Nutrient availability for soil microorganisms depends on the litter remaining after harvest; where slash (branches and other residue) is left on-site, C and N in the soil often increases as compared to pre-harvest conditions, whereas removal of whole trees tends to decrease them (Johnson and Curtis, 2001). Site with slash would then have more heterotrophic respiration (denitrification from denitrifiers), whereas whole-tree harvested sites would likely have lower emissions as they could only exhibit autotrophic respiration (nitrifier denitrification) (Wrage et al., 2001).

Soil changes occur not only from the removal of biomass, but also from the physical act of harvesting. Compaction from harvest machinery can make a soil less suitable for re-colonization by vegetation, as well as more likely to be improperly drained and therefore have anaerobic zones for gas production. Soils from skidder trails

at a temperate site in Germany were measured before and after harvesting, and exhibited up to 40 times more N_2O emissions and decreases in CH_4 oxidation by up to 90% (Teepe et al., 2004). The changes were attributed to decreases in macropore volume and increases in WFPS. It was noted, however, that the trails occupied a small percentage of the site, so that if traffic remained in these areas during successive harvesting events, the overall increase in emissions from the site would be minimal. Increases in N_2O emissions and decreases in CH_4 oxidation after logging have also been observed in Northern England (Zerva and Mencuccini, 2005), Florida (Castro et al., 2000), and Malaysia, where soils actually became a source of CH_4 (Yashiro et al., 2008).

Harvesting can also lead to significant water table increases in regions where vegetation was formerly acting as a control through evapotranspiration (Lavoie et al., 2005). This would be most common in peatland areas, especially those where the entire standing biomass was removed rather than only being partially harvested (Dube et al., 1995). Increased water tables have the potential to significantly increase both CH_4 and N_2O production (Regina et al., 1996; Jungkunst and Fiedler, 2007).

4.2.3 Cultivated forest soils

Cultivation has many of the same issues that are faced in forest harvesting, with the significant difference being the extent of the disturbance; unlike fire or harvest, cultivation is continuous. Compaction due to repeated traffic can increase both N_2O and CH_4 in cultivated soils and will tend to increase even more than in logged sites because agricultural soils are generally fertilized (Sitaula et al., 2000). In addition, repeated traffic over the site will cause more widespread compaction than is seen in most harvest blocks.

Many of the cultivated boreal soils in Europe are peatlands, which must be drained before use. However, peatland drainage has been shown to increase greenhouse gas emissions. Although draining the soil decreased the likelihood of CH_4 from the drained peat, Alm et al. (2007) noted that emissions from drainage ditches could more than make up for it. The drained peat also had the potential to increase N_2O production, but only on fertile or fertilized land; emissions were inversely correlated with C:N ratio.

Tillage maintained oxic conditions in the topsoil, which increased decomposition of N-rich organic matter, creating a low C:N ratio and increasing N_2O production (Alm et al., 2007).

The potential for increased emissions due to cultivation of forest stands is strongly dependent on texture. Since both denitrification and methanogenesis require anaerobic conditions, soils prone to holding water would be likely candidates for gas production. However, these are also the sites that would tend to be more fertile and therefore suitable for cultivation. Regina et al. (2007) studied CH_4 emissions from stands of varying textures and found that fluxes were correlated with the porosity of the soil. Macroporosity tended to increase oxidation, so that clay soils had the most emissions, followed by peat, and sandy loam had the least.

Another type of agriculture that makes use of boreal soils is animal agriculture. Maljanen et al. (2007) examined the effect of grazing on a pasture that had previously been forested, and found that both urine and dung more than doubled the N_2O emissions from the soils. Control plots emitted 11.4 ± 1.1 g N_2O-N ha^{-1} d^{-1}, whereas sites with urine and dung increased to 31.7 and 26.4 g N_2O-N ha^{-1} d^{-1} respectively. However, in pasture systems the spatial extent of urine and dung application was small as compared with the total field, and grassed areas in general were lower emitters of both N_2O and CH_4 than cropped or fallow fields. Maljanen et al. (2004) examined the differences between soils used for a variety of agricultural purposes and observed that grassed areas emitted 7.5 g N_2O-N ha^{-1} d^{-1} as compared to a barley crop (23.2 g N_2O-N ha^{-1} d^{-1}) and a fallow field (64.4 g N_2O-N ha^{-1} d^{-1}). CH_4 consumption was also noted to change, although less dramatically; grassed and cropped areas oxidized 2.7 g CH_4-C ha^{-1} d^{-1} whereas fallow fields only oxidized 1.5 mg CH_4-C ha^{-1} d^{-1}.

5. REFERENCES

Alm, J., Schulman, L., Walden, J., Nykanen, H., Martikainen, P. and Silvola, J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80: 161-174.

Alm, J., Shurpali, N.J., Minkkinen, K., Aro, L., Hytonen, J., Laurila, T., Lohila, A., Maljanen, M., Martikainen, P., Makiranta, P., Penttila, T., Saarnio, S., Silvan, N., Tuittila, E. and Laine, J. 2007. Emission factors and their uncertainty for the exchange of CO_2, CH_4 and N_2O in Finnish managed peatlands. Boreal Environ. Res. 12: 191-209.

Ambus, P., Zechmeister-Boltenstern, S. and Butterbach-Bahl, K. 2006. Sources of nitrous oxide emitted from European forest soils. Biogeosciences 3:135-146.

Arnold, K.v., Ivarsson, M., Oqvist, M., Majdi, H., Bjork, R.G., Weslien, P. and Klemedtsson, L. 2005. Can distribution of trees explain variation in nitrous oxide fluxes? Scand. J. For. Res. 20:481-489.

Balland, V., Bhatti, J., Errington, R., Castonguay, M. and Arp, P.A. 2006. Modeling snowpack and soil temperature and moisture conditions in a jack pine, black spruce and aspen forest stand in central Saskatchewan (BOREAS SSA). Can. J. Soil Sci. 86: 203-217.

Basiliko, N., Yavitt, J.B., Dees, P.M. and Merkel, S.M. 2003. Methane biogeochemistry and methanogen communities in two northern peatland ecosystems, New York State. Geomicrobiol. J. 20: 563-577.

Beckingham, J.D., Nielsen, D.G. and Futoransky, V.A. 1996. Field guide to ecosites of the mid-boreal ecoregions of Saskatchewan. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 6.

Bedard-Haughn, A., Matson, A.L. and Pennock, D.J. 2006. Land use effects on gross nitrogen mineralization, nitrification, and N_2O emissions in ephemeral wetlands. Soil Biol. Biochem. 38: 3398-3406.

Beland, M., Bergeron, Y. and Zarnovican, R. 2003. Harvest treatment, scarification and competing vegetation affect jack pine establishment on three soil types of the boreal mixed wood of northwestern Quebec. For. Ecol. Manage. 174: 477-493.

Bender, M. and Conrad, R. 1992. Kinetics of CH_4 oxidation in oxic soils exposed to ambient air or high CH_4 mixing ratios. FEMS Microbiol. Ecol. 101:261-270.

Bender, M. and Conrad, R. 1994. Methane oxidation activity in various soils and freshwater sediments: occurrence, characteristics, vertical profiles and distribution on grain size fraction. J. Geophys. Res. 99: 16531-16540.

Bengtsson, G., Bengtson, P. and Mansson, K.F. 2003. Gross nitrogen mineralization-, immobilization-, and nitrification rates as a function of soil C/N ratio and microbial activity. Soil Biol. Biochem. 35: 143-154.

Berestovskaya, Y.Y., Rusanov, I.I., Vasil'eva, L.V. and Pimenov, N.V. 2005. The processes of methane production and oxidation in the soils of the Russian arctic tundra. Microbiology 74: 261-270.

Bodelier, P.L.E. and Frenzel, P. 1999. Contribution of methanotrophic and nitrifying bacteria to CH_4 and NH_4 oxidation in the rhizosphere of rice plants as determined by new methods of discrimination. Appl. Environ. Microbiol. 65:1826-1833.

Booth, M.S., Stark, J.M. and Rastetter, E. 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. Ecol. Monogr. 75: 139-157.

Borken, W. and Beese, F. 2005. Control of nitrous oxide emissions in European beech, Norway spruce and Scots pine forests. Biogeochemistry 76: 141-159.

Brumme, R., Borken, W. and Finke, S. 1999. Hierarchical control on nitrous oxide emission in forest ecosystems. Glob. Biogeochem. Cycles 13: 1137-1148.

Busenberg, G. 2004. Wildfire management in the United States: the evolution of a policy failure. Rev. Policy Res. 21: 145-156

Carmosini, N., Devito, K.J. and Prepas, E.E. 2002. Gross nitrogen transformations in harvested and mature aspen-conifer mixed forest soils from the boreal plain. Soil Biol. Biochem. 34: 1949-1951.

Castro, M.S., Gholz, H.L., Clark, K.L. and Steudler, P.A. 2000. Effects of forest harvesting on soil methane fluxes in Florida slash pine plantations. Can. J. For. Res. 30: 1534–1542.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143: 1-10.

Chen, Y. and Hogeberg, P. 2006. Gross nitrogen mineralization rates still high 14 years after suspension of N input to a N-saturated forest. Soil Biol. Biochem. 38: 2001-2003.

Chidthaisong, A. and Conrad, R. 2000. Turnover of glucose and acetate coupled to reduction of nitrate, ferric iron and sulfate and to methanogenesis in anoxic rice field soil. FEMS Microbiol. Ecol. 31:73-86.

Dalton, H. and R. Brand-Hardy. 2003. Nitrogen: the essential public enemy. J. Appl. Ecol. 40:771-781.

Davidson, E.A., Hart, S.C. and Firestone, M.K. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology 73: 1148-1156.

Davidson, E.A., Hart, S.C., Shanks, C.A. and Firestone, M.K. 1991. Measuring gross nitrogen mineralization, immobilization, and nitrification by N-15 isotopic pool dilution in intact soil cores. J. Soil Sci. 42: 335-349.

DeLuca, T.H., MacKenzie, M.D., Gundale, M.J. and Holben, W.E. 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. Soil Sci. Soc. Am. J. 70: 448-453.

Driscoll, C.T. 2003. Elevated inputs of reactive nitrogen in the environment causes, consequences, and controls. BioScience 53:311.

Dubé, S., Plamondon, A.P. and Rothwell, R.L. 1995. Watering-up after clear-cutting on forested wetlands on the St. Lawrence lowland. Water Resour. Res. 31: 1741-1750.

Environment Canada. 2003. Environmental signals: Canada's national environmental indicator series [Online]. pgs. 44-46. Available at http://www.ec.gc.ca/soer-ree (verified 31 July, 2008).

Environment Canada (Greenhouse Gas Division). 2007. National inventory report 1990-2005: greenhouse gas sources and sinks in Canada [Online]. pgs. 7-54. Available at http://www.ec.gc.ca/ghg-ges (verified 24 July, 2008).

Environment Canada. 2008. Monthly data reports for 1947-2007 [Online]. Available at http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html (verified 21 September, 2008).

Fluxnet Canada Data Information System, 2007. Canadian Carbon Program/Fluxnet-Canada Research Network [Online]. Available at: http://fluxnet.ccrp.ec.gc.ca/e_DataAccess.htm (verified 20 August, 2008).

Fluxnet Canada Data Information System, 2008. Canadian Carbon Program/Fluxnet-Canada Research Network [Online]. Available at: http://fluxnet.ccrp.ec.gc.ca/e_DataAccess.htm (verified 20 August, 2008).

Gutsell, S. and Johnson, E. 2005. Potential causes of a post-fire conversion of forest to non-forest in the boreal forest, Saskatchewan. *In* Abstracts, Annu. Meet., Ecological Society of America, Montreal, QC. 4-12 Aug. 2005. Ecol. Soc. Am., Montreal, QC.

Harrison, K.A., Bol, R. and Bardgett, R.D. 2007. Preferences for different nitrogen forms by coexisting plant species and soil microbes. Ecology 88: 989-999.

Harrison, K.A., Bol, R. and Bardgett, R.D. 2008. Do plant species with different growth strategies vary in their ability to compete with soil microbes for chemical forms of nitrogen? Soil Biol. Biochem. 40: 228-237.

Hart, S.C., Stark, J.M., Davidson, E.A. and Firestone, M.K. Nitrogen mineralization, immobilization, and nitrification. In: R. Weaver (ed.), Methods of Soil Analysis, Part 2. Microbiological and Biochemical Properties. SSSA Book Series, No. 5, American Society of Agronomy, Madison, WI (1994), pp. 985–1019.

Heitmann, T., Goldhammer, T., Beer, J. and Blodau, C. 2007. Electron transfer of dissolved organic matter and its potential significance for anaerobic respiration in a northern bog. Glob. Change Biol. 13: 1771-1785.

Hoehler, T.M., Alperin, M.J., Albert, D.B. and Martens, C.S. 1994. Field and laboratory studies of methane oxidation in an anoxic marine sediment - evidence for a methanogen-sulfate reducer consortium. Glob. Biogeochem. Cycles 8: 451-463.

Hogberg, M.N., Myrold, D.D., Gieler, R. and Hogberg, P. 2006. Contrasting patterns of soil N-cycling in model ecosystems of Fennoscandian boreal forests. Oecologia 147: 96-107.

Hogg, E. H., Lieffers, V.J. and Wein, R.W. 1992. Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. Ecol. Appl. 2: 298-306.

Hornibrook, E.R.C., Longstaffe, F.J. and Fyfe, W.S. 1997. Spatial distribution of microbial methane production pathways in temperate zone wetland soils: stable carbon and hydrogen isotope evidence. Geochimica Cosmochim. Acta 61: 745-753.

Huber, R., Kurr, M., Jannasch, H.W. and Stetter, K.O. 1989. A novel group of abyssal methanogenic archaebacteria (*Methanopyrus*) growing at 110 °C. Nature 342: 833-834.

Huttunen, J.T., Nykanen, H., Turunen, J. and Martikainen, P.J. 2003. Methane emissions from natural peatlands in the northern boreal zone in Finland, Fennoscandia. Atmos. Environ. 37: 147-151.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

IPCC. 2007. Climate change 2007: the scientific basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Johnson, D.W. and Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manage. 140: 227-238.

Johnson, D., Kershaw, L., MacKinnon, A. and Pojar, J. 1995. Plants of the western boreal forest and aspen parkland. Lone Pine Publishing, Edmonton, AB.

Jones, D.L., Healey, J.R., Willett, V.B., Farrar, J.F. and Hodge, A. 2005. Dissolved organic nitrogen uptake by plants - an important N uptake pathway? Soil Biol. Biochem. 37: 413-423.

Jones, D.L. and Kielland, K. 2002. Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. Soil Biol. Biochem. 34: 209-219.

Jugnia, L., Roy, R., Planas, D., Lucotte, M. and Greer, C.W. 2005. Activité potentielle de méthanogenèse dans les sols, tourbières, sédiments lacustres et du réservoir hydroélectrique Rober-Bourassa dans le moyen Nord-Canadien. Can. J. Microbiol. 51: 79-84.

Jungkunst, H.F. and Fiedler, S. 2007. Latitudinal differentiated water table control of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change. Glob. Change Biol. 13: 2668-2683.

Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. Ecology 75: 2373-2383.

Kielland, K., McFarland, J. and Olson, K. 2006. Amino acid uptake in deciduous and coniferous taiga ecosystems. Plant Soil 288: 297-307.

Kielland, K. McFarland, J.W., Ruess, R.W. and Olson, K. 2007. Rapid cycling of organic nitrogen in taiga forest ecosystems. Ecosystems 10: 360-368.

Kemball, K.J., Wang, G.G. and Dang, Q. 2005. Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. Can. J. Bot. 83: 1550-1560.

Kranabetter, J.M., Dawson, C.R. and Dunn, D.E. 2007. Indices of dissolved organic nitrogen, ammonium and nitrate across productivity gradients of boreal forests. Soil Biol. Biochem. 39: 3147-3158.

Larsen, C.P.S. 1996. Fire and climate dynamics in the boreal forest of northern Alberta, Canada, from AD 1850 to 1989. Holocene 6: 449-456.

Lavoie, M., Pare, D., Fenton, N., Groot, A. and Taylor, K. 2005. Paludification and management of forested peatlands in Canada : a literature review. Environ. Rev. 13: 21-50.

Le Mer, J. and Roger, P. 2001. Production, oxidation, emission and consumption of methane by soils: a review. Eur. J. Soil Biol. 37:25-50.

Lemke, R.L., Izaurralde, R.C. and Nyborg, M. 1998. Seasonal distribution of nitrous oxide emissions from soils in the parkland region. Soil Sci. Soc. Am. J. 62:1320-1326.

Lemmen, D.S. and Warren, F.J. (eds) 2004. Climate change impacts and adaptation: a Canadian perspective [Online]. Availabe at: http://adaptation.nrcan.gc.ca/pub_e.php (verified 31 July, 2008).

Levine, J.S., Cofer, W.R., Sebacher, D.I., Rhinehart, R.P., Winstead, E.L., Sebacher, S., Hinkle, C.R., Schmalzer, P.A. and Koller, A.M. 1990. The effects of fire on biogenic emissions of methane and nitric oxide from wetlands. J. Geophys. Res. 95: 1853-1864.

Liebner, S. and Wagner, D. 2007. Abundance, distribution and potential activity of methane oxidizing bacteria in permafrost soils from the Lena Delta, Siberia. Environ. Microbiol. 9:107-117.

Ludwig, B., Teepe, R., Lopes de Gerenyu, V. and Flessa, H. 2006. CO_2 and N_2O emissions from gleyic soils in the Russian tundra and a German forest during freeze-thaw periods - a microcosm study. Soil Biol. Biochem. 38: 3516-3519.

Maljanen, M., Komulainen, V.M., Hytonen, J., Martikainen, P.J. and Laine, J. 2004. Carbon dioxide, nitrous oxide and methane dynamics in boreal organic agricultural soils with different soil characteristics. Soil Biol. Biochem. 36: 1801-1808.

Maljanen, M., Martikkala, M., Koponen, H.T., Virkajarvi, P. and Martikainen, P.J. 2007. Fluxes of nitrous oxide and nitric oxide from experimental excreta patches in boreal agricultural soil. Soil Biol. Biochem. 39: 914-920.

Matthews, C.J.D., Joyce, E.M., St. Louis, V.L., Schiff, S.L., Venkiteswaran, J.J., Hall, B.D., Bodaly, R.A. and Beaty, K.G. 2005. Carbon dioxide and methane production in small reservoirs flooding upland boreal forest. Ecosystems 8: 267-285.

MapQuest. 2008. Road map of northern Saskatchewan [Online]. Available at: http://www.mapquest.com/maps?city=Prince+Albert&state=SK (verified 31 July, 2008).

Mayer, H.P. and Conrad, R. 1990. Factors influencing the population of methanogenic bacteria and the initiation of methane production upon flooding of paddy soil. FEMS Microbiol. Ecol. 73:103-112

Moore, T.R. and Basiliko, N. 2006. Decomposition in boreal peatlands. pg. 125-139. *In* R.K. Wieder and D.H. Vitt (eds.) Boreal Peatland Ecosystems. Springer-Verlag, Berlin, Heidelberg.

Moore, T.R. and Dalva, M. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J. Soil Sci. 44: 651-664.

Moore, T.R. and Knowles, R. 1990. Methane emissions from fen, bog and swamp peatlands in Quebec. Biogeochemistry 11: 45-61.

Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M. and Hogberg, P. 1998. Boreal forest plants take up organic nitrogen. Nature 392: 914-916.

Näsholm, T. and Persson, J. 2001. Plant acquisition of organic nitrogen in boreal forests. Physiol. Plant. 111: 419-426.

Natural Resources Canada (Canada Centre for Remote Sensing GeoAccess Division). 2001. Land and freshwater areas [Online]. Available at: http://atlas.nrcan.gc.ca/site/english/learningresources/facts/surfareas.html (verified 31 July, 2008).

Nitschke, C.R. 2005. Does forest harvesting emulate fire disturbance? A comparison of effects on selected attributes in coniferous-dominated headwater systems. For. Ecol. Manage. 214: 305-319.

Nordin, A., Hogberg, P. and Näsholm, T. 2001. Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. Oecologia 129: 125-132.

Nordin, A., Schmidt, I.K. and Shaver, G.R. 2004. Nitrogen uptake by arctic soil microbes and plants in relation to soil nitrogen supply. Ecology 85: 955-962.

Oquist, M.G., Nilsso, M., Sorensson, F., Kasimir-Klemedtsson, A., Persson, T., Weslien, P. and Klemedtsson, L. 2004. Nitrous oxide production in a forest soil at low temperatures - processes and environmental controls. FEMS Microbiol. Ecol. 49: 371-378.

Oquist, M.G., Petrone, K., Nilsson, M. and Klemedtsson, L. 2007. Nitrification controls N_2O production rates in a frozen boreal forest soil. Soil Biol. Biochem. 39: 1809-1811.

Paavolainen, L. 1999. Nitrogen transformations in boreal forest soils in response to extreme manipulation treatments [Online]. Available at http://ethesis.helsinki.fi/julkaisut/maa/skemi/vk/paavolainen/nitrogen.html (verified 31 July, 2008).

Persson, J., Hogberg, P., Ekblad, A., Hogberg, M., Nordgren, A. and Näsholm, T. 2003. Nitrogen acquisition from inorganic and organic sources by boreal forest plants in the field. Oecologia 137: 252-257.

Persson, J. and Näsholm, T. 2001. Amino acid uptake: a widespread ability among boreal forest plants. Ecol. Lett. 4: 434-438.

Pihlatie, M., Pumpanen, J. Rinne, J., Ilvesniemi, H., Simojoki, A., Hari, P. and Vesala, T. 2007. Gas concentration driven fluxes of nitrous oxide and carbon dioxide in boreal forest soil. Tellus: Series B 59: 458-469.

Phipps, K.J. 2006. Spatial and temporal variation in greenhouse gas emissions from two open water prairie wetlands. M.Sc. thesis. Univ. of Saskatchewan, Saskatoon, SK.

Poth M. and Focht D.D. 1985. 15N kinetic analysis of N2O production by *Nitrosomonas europaea*: an examination of nitrifier denitrification. Appl. Environ. Microbiol. 49: 1134-1141.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51: 73-108.

Raison R.J., Connell M.J. and Khanna P.K. 1987. Methodology for studying fluxes of soil mineral-N in situ. Soil Biol. Biochem. 19: 521-530.

Rask, H., Schoenau, J. and Anderson, D. 2002. Factors influencing methane flux from a boreal forest wetland in Saskatchewan, Canada. Soil Biol. Biochem. 34: 435-443.

Regina, K., Nykanen, H., Silvola, J. and Martikainene, P.J. 1996. Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry 35: 401-418.

Regina, K., Pihlatie, M., Esala, M. and Alakukku, L. 2007. Methane fluxes on boreal arable soils. Agric. Ecosyst. Environ. 119:346-352.

Renault, P., and Stengel, P. 1994. Modeling oxygen diffusion in aggregated soils: I. anaerobiosis inside the aggregate. Soil Sci. Soc. Am. J. 58: 1017-1023.

Ritchie, D.A., Edwards, C., McDonald, I.R. and Murrell, J.C. 1997. Detection of methanogens and methanotrophs in natural environments. Glob. Change Biol. 3: 339-350.

Rodionow, A., Flessa, H., Kazansky, O. and Guggenberger, G. 2006. Organic matter composition and potential trace gas production of permafrost soils in the forest tundra in northern Siberia. Geoderma 135: 49-62.

Saari, A., Martikainen, P.J., Ferm, A., Ruuskanen, J., De Boer, W., Troelstra, S.R. and Laanbroek, H.J. 1997. Methane oxidation in soil profiles of Dutch and Finnish coniferous forests with different soil texture and atmospheric nitrogen deposition. Soil Biol. Biochem. 29: 1625-1632.

Saarnio, S., Morero, M., Shurpali, N.J., Tuittila, E., Makila, M. and Alm, J. 2007. Annual CO_2 and CH_4 fluxes of pristine boreal mires as a background for the lifecycle analyses of peat energy. Boreal Environ. Res. 12: 101-113.

Saskatchewan Forest Centre. 2006. Saskatchewan Facts on Wood Series [Online]. Available at: http://www.saskforestcentre.ca/index.php?f=content&c=169 (verified August 24, 2008).

Schimel, J.P. and Bennett, J. 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85: 591–602.

Schimel, J.P. and Chapin, F.S. 1996. Tundra plant uptake of amino acid and NH_4^+ nitrogen in site: plants compete well for amino acid N. Ecology 77:2142-2147.

Sitaula, B.K., Hansen, S., Sitaula, J.I.B. and Bakken, L.R. 2000. Methane oxidation potentials and fluxes in agricultural soil: effects of fertilization and soil compaction. Biogeochemistry 48: 323-339.

Smemo, K.A. and Yavitt, J.B. 2007. Evidence for anaerobic CH_4 oxidation in freshwater peatlands. Geomicrobiol. J. 24: 583-597.

Smith, N.R., Kishchuk, B.E. and Mohn, W.W. 2008. Effects of wildfire and harvest disturbances on forest soil bacterial communities. Appl. Environ. Microbiol. 74: 216-224.

Sparks, D.L. 2003. Environmental soil chemistry, second edition. Academic Press, San Diego, CA 92101-4495.

Startsev, N.A. and Lieffers, V.J. 2007. Emission of nitrogen gas, nitrous oxide, and carbon dioxide on rehydration of dry feathermoss. Soil Sci. Soc. Am. J. 71: 214-218.

Stark, J.M. and Hart, S.C. 1996. Diffusion technique for preparing salt solutions, Kjeldahl digests, and persulfate digests for nitrogen-15 analysis. Soil Sci. Soc. Am. J. 60: 1846-1855.

Steudler, P.A., Melillo, J.M., Feigl, B.J., Neill, C., Piccolo, M.C. and Cerri, C.C. 1996. Consequence of forest-to-pasture conversion on CH_4 fluxes in the Brazilian Amazon Basin. J. Geophys. Res. Atmos. 101: 18547-18554.

Stevens, R.J., Laughlin, R.J., Burns, L.C., Arah, J.R.M. and Hood, R.C. 1997. Measuring the contributions of nitrification and denitrification to the flux of nitrous oxide from soil. Soil Biol. Biochem. 29: 139–151.

Sullivan, B.W., Kolb, T.E., Hart, S.C., Kaye, J.P., Dore, S. and Montes-Helu, M. 2008. Thinning reduces soil carbon dioxide but not methane flux from southwestern USA ponderosa pine forests. For. Ecol. Manage. 255: 4047-4055.

Taylor, A.F.S., Gebauer, G. and Read, D.J. 2004. Uptake of nitrogen and carbon from double-labeled (^{15}N and ^{13}C) glycine by mycorrhizal pine seedlings. New Phytol. 164:383-388.

Teepe, R., Brumme, R., Beese, F. and Ludwig, B. 2004. Nitrous oxide emission and methane consumption following compaction of forest soils. Soil Sci. Soc. Am. J. 68: 605–611.

Teepe, R. and Ludwig, B. 2004. Variability of CO_2 and N_2O emissions during freeze-thaw cycles: results of model experiments on undisturbed forest-soil cores. J. Plant Nutr. Soil Sci. 167: 153-159.

Valentine, D.L. 2002. Biogeochemistry and microbial ecology of methane oxidation in anoxic environments: a review. Antonie van Leeuwenhoek 81: 271-282.

Vasander, H. and Kettunen, A. 2006. Carbon in boreal peatlands. pg. 1625-180. *In* R.K. Wieder and D.H. Vitt (eds.) Boreal Peatland Ecosystems. Springer-Verlag, Berlin, Heidelberg.

Veldkamp, E., Keller, M. and Nunez, M. 1998. Effects of pasture management on N_2O and NO emissions from soils in the humid tropics of Costa Rica. Glob. Biogeochem. Cycles 12:71-79.

Vitousek, P.M., Matson, P.A. and van Cleve, K. 1989. Nitrogen availability and nitrification during succession: primary, secondary and old-field seres. Plant Soil 115: 229-239.

Waddington, J.M. and Roulet, N.T. 2000. Carbon balance of a boreal patterned peatland. Glob. Change Biol. 6: 87-97.

Wagner-Riddle, C. and Thurtell, G.W. 1998. Nitrous oxide emissions from agricultural fields during winter and spring thaw as affected by management practices. Nutr. Cycling Agroecosyst. 52:151-163.

Weir, J.M.H and Johnson, E.A. 1998. Effects of escaped settlement fires and logging on forest composition in the mixedwood boreal forest. Can. J. For. Res. 28:459-467.

Westbrook, C.J. and Devito, K.J. 2004. Gross nitrogen transformations in soils from uncut and cut boreal upland and peatland coniferous forest stands. Biogeochemistry 68: 33-50.

Westbrook, C.J., Devito, K.J. and Allen, C.J. 2006. Soil N cycling in harvested and pristine boreal forests and peatlands. Forest Ecol. and Manage. 234: 227-237.

Whalen, S.C. 2005. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. Environ. Engineering Sci. 22: 73-94.

Whalen, S.C. and Reeburgh, W.S. 2000. Methane oxidation, production, and emission at contrasting sites in a boreal bog. Geomicrobiol. J. 17: 237-251.

Whalen, S.C., Reeburgh, W.S. and Barber, V.A. 1992. Oxidation of methane in boreal forest soils: a comparison of seven measures. Biogeochemistry 16: 181-211.

Whiticar, M.J., Faber, E. and Schoell, M. 1986. Biogenic methane formation in marine and fresh-water environments - CO_2 reduction vs. acetate fermentation isotope evidence. Geochim. Cosmochim. Acta 50: 693-709.

Wrage, N., Velthof, G.L., van Beusichem, M.L. and Oenema, O. 2001. Role of nitrifier denitrification in the production of nitrous oxide. Soil Biol. Biochem. 33:1723-1732.

Wray, H.E. and Bayley, S.E. 2007. Denitrification rates in marsh fringes and fens in two boreal peatlands in Alberta, Canada. Wetlands 27: 1036-1045.

Yashiro, Y., Kadir, W.R., Okuda, T. and Koizumi, H. 2008. The effects of logging on soil greenhouse gas (CO_2, CH_4, N_2O) flux in a tropical rain forest, Peninsular Malaysia. Agric. For. Meteorol. 148: 799-806.

Yates, T.T., Si, B.C., Farrell, R.E. and Pennock, D.J. 2006. Probability distribution and spatial dependence of nitrous oxide emission: temporal change in hummocky terrain. Soil Sci. Soc. Am. J. 70:753-762.

Zackrisson, O., Nilsson, M. and Wardle, D. 1996. Key ecological function of charcoal from wildfire in the boreal forest. Oikos 77: 10-19.

Zerva, A. and Menuccini, M. 2005. Short-term effects of clearfelling on soil CO_2, CH_4, and N_2O fluxes in a Sitka spruce plantation. Soil Biol. Biochem. 37:2025-2036.

Zoltai, S.C., Morrissey, L.A., Livingston, G.P. and de Groot, W.J. 1998. Effects of fires on carbon cycling in North American boreal peatlands. Environ. Rev. 6: 13-24.

6. APPENDIX

Appendix A: Locations and water chemistry of sampling sites within the White Swan Upland ecodistrict, where the OBS site from this study was located.

Table A.1. Location and water body types of sampling sites in the White Swan Upland ecodistrict of Saskatchewan.

Site Name	GPS coordinates (m)		Water Body Type
	Easting	Northing	
OBS site 4	0492458	5982168	Seasonal Wetland
OBS site 7	0492458	5982168	Seasonal Wetland
OBS site 16	0492458	5982168	Seasonal Wetland
OBS site 17	0492458	5982168	Seasonal Wetland
Lost Creek	0472838	5989686	Creek/River
Hanin Creek	0470857	5974471	Creek/River
Clearsand Creek	0464279	5967734	Creek/River
Candle Lake	0477534	5961703	Lake
Torch Lake	0481275	5955939	Lake
East Trout Lake	0501741	6022952	Lake
Clarence Lake	0500259	6010657	Lake
Kit Lake	0498769	6011754	Lake
Jasper Lake	0496694	6011969	Lake
Ridge Lake	0497953	6012078	Lake
Piprell Lake	0506356	6000571	Lake
Moose River	0501603	5999811	Creek/River
Wetland on 913	0496703	5990959	Seasonal Wetland
Pinkney Lake	0495776	5988042	Lake
Whelan Bay	0492394	5986716	Lake
Creek near road	0483170	5986578	Creek/River
Heritage Lake	0490538	5975506	Lake
White Gull Creek North	0513774	5975185	Creek/River

Note: this data is courtesy of Cara Drury, 2008 (unpublished).

Table A.2. Water chemistry from wetlands in the White Swan Upland ecodistrict of Sasakatchewan in July, 2007.

Site Name	pH	E.C.	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	Cl^{-}	SO_4^{2-}
		µS/cm	----------mg/L----------					
Lost Creek	7.91	0.49	27.73	24.65	6.22	2.81	0.73	1.68
Hanin Creek	8.06	0.26	25.71	13.07	4.30	1.01	1.44	1.98
Clearsand Creek	8.73	0.33	19.82	18.20	6.86	3.11	1.56	2.65
Candle Lake	7.49	0.32	20.57	19.07	9.20	3.75	4.89	4.91
Torch Lake	8.84	0.33	27.32	19.34	8.67	3.47	3.88	4.68
East Trout Lake	8.13	0.23	14.85	8.40	2.81	1.10	1.80	1.27
Clarence Lake	7.50	0.30	18.33	11.34	4.54	1.95	0.85	1.40
Kit Lake	8.50	0.13	7.90	4.84	1.96	1.11	0.85	2.31
Jasper Lake	8.02	0.22	22.52	9.77	3.25	0.97	0.49	1.40
Ridge Lake	7.59	0.22	15.75	7.54	2.77	1.42	0.85	1.40
Piprell Lake	7.44	0.27	16.02	16.19	2.96	2.57	0.73	2.14
Moose River	7.58	0.24	17.37	10.49	2.48	1.02	0.49	1.54
Wetland on 913	6.89	0.08	6.58	4.05	1.10	4.05	1.09	1.98
Pinkney Lake	8.96	0.14	11.15	6.00	1.56	2.68	2.53	1.02
Whelan Bay	7.65	0.24	8.56	13.72	4.32	3.77	-	0.91
Creek near road	6.35	0.16	18.88	7.30	2.47	3.42	1.21	2.14
Heritage Lake	7.54	0.37	15.33	25.40	10.29	4.61	1.80	1.54
White Gull Creek	7.43	0.02	20.10	7.63	5.13	0.57	3.26	2.48
OBS site 4	6.06	0.09	14.01	5.03	1.39	0.30	2.89	25.31
OBS site 7	6.41	0.11	10.25	4.07	0.51	0.11	2.77	39.65
OBS site 16	6.75	0.29	21.86	8.25	1.26	0.43	3.51	9.58
OBS site 17	6.71	0.28	35.48	13.94	0.84	0.69	1.44	13.24
Average	**7.57**	**0.23**	**18.00**	**11.74**	**3.86**	**2.04**	**1.86**	**5.69**
Std. Deviation	0.81	0.11	7.13	6.41	2.82	1.41	1.25	9.43

Note: this data is courtesy of Cara Drury, 2008 (unpublished).